LARVAL FISH ASSEMBLAGES IN COASTAL, SHELF AND OFFSHORE WATERS OF SOUTH-WESTERN AUSTRALIA

Barbara A. Muhling

This thesis is presented for the degree of Doctor of Philosophy

in the School of Environmental Science,

Murdoch University

June 2006

Declaration

I declare that this thesis is my own account of my research and contains, as its main content, work which has not previously been submitted for a degree at any tertiary education institution

Abstract

Larval fish assemblages were investigated during a three-year multidisciplinary project conducted off the coast of south-western Australia. Larvae were sampled using replicated oblique bongo net tows along a five-station transect extending from inshore (18m depth) to offshore waters (1000m depth). A total of 148 taxa from 93 teleost families were identified. Larvae of Gobiidae, and Blenniidae were abundant inshore, while larvae of pelagic and reef-dwelling families, such as Clupeidae, Engraulidae, Carangidae and Labridae were common in continental shelf waters. Larvae of oceanic families, particularly Myctophidae, Phosichthydae and Gonostomatidae, dominated offshore assemblages. Inshore larval fish assemblages were the most seasonal, in terms of species composition and abundance, with offshore assemblages the least so.

Multivariate statistical analyses revealed larval fish assemblages to have a strong temporal and spatial structure. Assemblages were closely correlated to water masses, with species distributions reflecting both cross-shelf and along-shore oceanographic processes and events. The strength and position of the warm, southward flowing Leeuwin Current, and of the cool, seasonal, northward flowing Capes Current were shown to drive much of the variability in the marine environment, and thus larval fish assemblages.

Many of the distinctions between larval fish assemblages on the continental shelf were attributable to patterns of abundance in clupeiform larvae. While larvae of *Engraulis australis* and *Spratelloides robustus* showed clear seasonal and spatial distribution patterns, larvae of *Sardinops sagax* and *Etrumeus teres* were found

throughout the year, with high interannual variability in abundance. Abundances of larvae from all pelagic clupeiform species were negatively correlated to microzooplankton concentrations. Peaks of abundance of *S. sagax* and *E. teres*, in particular, appeared to be better aligned with favourable transport and retention conditions.

A detailed comparison of the horizontal and vertical distribution of larval fishes highlighted the influence of contrasting oceanographic conditions between summer and winter on larval fish assemblages. Although most fish larvae were found above the thermocline, depth distributions differed between taxa, and were shown to influence their offshore transport. Neustonic fish larvae showed potential for significant dispersion during summer, as a result of offshore Ekman transport.

Mesoscale Leeuwin Current eddies were a feature of the oceanography of the region, and their influence on larval fish assemblages was examined in both an anti-cyclonic eddy (warm-core) and a cyclonic eddy (cold-core). The warm-core eddy contained larval fish assemblages that were distinct from those in the cold-core eddy, with lower larval fish concentrations, especially in the eddy centre. Although the eddies originated near the continental shelf, larval fish assemblages within both eddies were largely oceanic, probably a result of the age of the eddies when they were sampled (about 5 months).

Overall, larval fish assemblages showed strong temporal and spatial structure, and were well aligned to water masses in the region. The unique oceanography off south-

western Australia thus has considerable implications for both larval fish transport, and potential recruitment to regional fisheries.

Acknowledgements

I would like to thank Tony Miskiewicz, Pilar Olivar, Francisco Neira, Tom Trnski and Jeff Leis for their invaluable help with identifying fish larvae. No fish too small…

Alan Pearce, Nick Mortimer, Chris Fandry and Peter Fearns provided much help with oceanographic data and interpretation, and are thanked for their input, and patience. Joanna Strzelecki, Stephane Pesant and Hiski Kippo are thanked for providing access to data, data organisation and helpful interpretation of datasets. Fiona Valesini provided invaluable help with the use of Primer-6, the interpretation of results, and statistics generally.

Anya Waite is thanked for providing leadership and organisation on the eddies cruise, and for help with interpretation of oceanographic and biological data. Warren Chisholm provided neuston net data, and helpful discussions, and Chris Jones helped with conclusions in relation to his sardine otolith data, as part of his Masters project.

Tony Koslow and the rest of the SRFME Biophysical Oceanography team are thanked for putting in many hours of hard work to collect samples on the Two Rocks transect for three years, often in trying conditions. Harriet Paterson provided microzooplankton data, insightful discussions, and generally good company. Dan Gaughan helped with data interpretation for Chapter 4, and provided valuable feedback on written work, and supplied sardine GSI data, in association with Tim Leary, and the Department of Fisheries, Western Australia.

Matt Harvey and Dave Holliday are thanked for providing general distractions. Jill and Janet Muhling are to be acknowledged for setting a precedent for PhD submission in the family, and my parents are both thanked for all support and encouragement. Nick Barratt provided limitless moral support, and put up with me in general. My principal supervisor, Lynnath Beckley, is thanked for her substantial hard work and boundless energy put into both the larval fish project, and into the reading and correction of this thesis. Tony Koslow is also thanked for his supervision, both of this project, and the SRFME Biophysical Oceanography project, and comments on written work.

The Strategic Research Fund for the Marine Environment, CSIRO and Murdoch University are acknowledged for scholarship funding, and research support. The masters and crews of the *RV Southern Surveyor, Naturaliste, Maritime Image* and *Mesocat* are also thanked for help and expertise in field operations.

Table of Contents

Chapter 1: Introduction

1.1 The unique oceanographic conditions off south-western Australia

The ocean off south-western Australia has a number of distinctive, sometimes unusual characteristics. The waters are relatively clear and well-mixed, with low nutrient concentrations, due a lack of upwelling in the region, and little terrestrial runoff (Lenanton *et al.*, 1991; Johannes *et al.*, 1994). Many of these features are a direct result of the regional eastern boundary current; the Leeuwin Current (Figure 1.1).

Unlike other eastern boundary currents, such as those off South America, southern Africa and California, the Leeuwin Current flows poleward (Cresswell, 1991). The current is driven by an alongshore stearic height gradient, due to the interconnection between the Pacific and Indian Oceans through the Indonesian Archipelago, which overwhelms the opposing equatorwards wind stress. The eastward flow in the upper ocean layer generated by this poleward flow is stronger than the westward wind-driven Ekman flow and results in downwelling along the coast (Pearce and Pattiaratchi, 1999). As these conditions result in the suppression of upwelling, there are consequently low nutrient concentrations, and low phytoplankton productivity in local coastal waters (Hanson *et al.*, 2005; Lourey *et al.*, 2006). This leads to finfish production of virtually insignificant proportions when compared to that of the Benguela Current off South Africa, or the Humboldt Current of South America (Lenanton *et al.*, 1991).

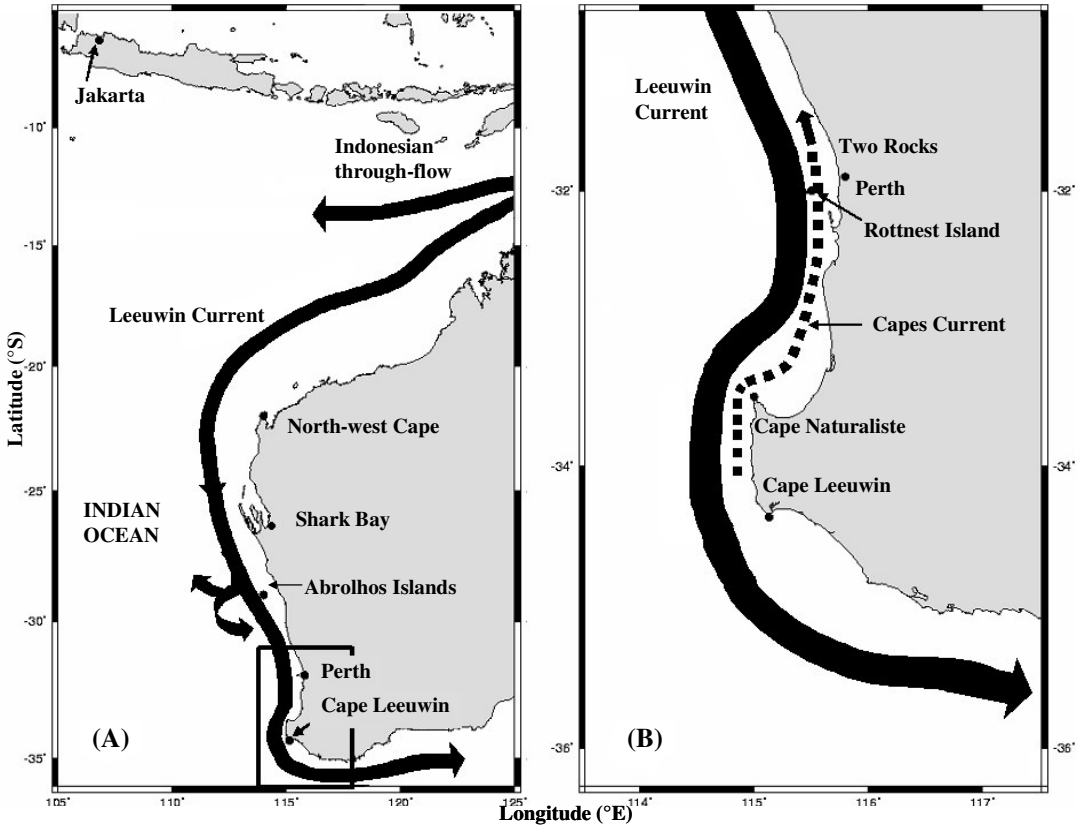

Figure 1.1: Schematic diagram showing (A): the approximate location and direction of flow of the Leeuwin Current off the coast of Western Australia, and (B): the position and direction of flow of the Leeuwin Current and Capes Current off south-western Australia. Adapted from Online Map Creation.

The Leeuwin Current is recognizable as a stream of warm, low salinity water, flowing southwards over the continental shelf from around the North West Cape (Woo *et al*., 2006). It moves off the shelf at about 27° South, passing to the west of the Abrolhos Islands and Rottnest Island. It then rounds Cape Leeuwin, and flows eastwards across the Great Australian Bight (Cresswell, 1991; Ridgway and Condie, 2004). The Leeuwin Current flows strongest in autumn and winter, and weakest from November to March, when southerly winds create a strong equator-ward wind stress (Gersbach *et al*., 1999). It results in the southward extension of the ranges of many tropical species,

by providing warmer water temperatures than would otherwise be present, and by acting as a southwards conduit for larvae of tropical species (Hutchins, 1991; Hutchins and Pearce, 1994). The eddy kinetic energy of the Leeuwin Current is the highest of any eastern boundary current (Feng *et al*., 2005). As a result, both cyclonic and anti-cyclonic eddies are commonly formed in association with the current (Morrow *et al.*, 2003). Mesoscale jets, undulations and meanders of the Leeuwin Current are also a common occurrence (Pearce and Griffiths, 1991), and such features may significantly influence the response of adjacent continental shelf waters.

The Leeuwin Current largely suppresses upwelling along the south-west Australian coast. However, when strong southerly winds prevail during summer, a small upwelling feature may be present on the shelf between Cape Naturaliste and Cape Leeuwin (Figure 1.1). Under the influence of southerly winds, this feature may extend northwards as a narrow, cooler stream of water inshore of the weakened Leeuwin Current. This feature is now known as the Capes Current (Gersbach *et al*., 1999; Pearce and Pattiaratchi, 1999). The biological effects of this current are not well known, but it does not appear to significantly increase nutrient and productivity levels in the region, as the water upwelled is mostly sourced from the base of the nutrient-poor Leeuwin Current (Gersbach *et al*., 1999; Hanson *et al.*, 2005).

Both the Leeuwin and Capes Currents introduce complexities into the largely oligotrophic coastal waters off south-west Western Australia. They allow the transport of planktonic organisms, and warmer or cooler water away from their points of origin, and result in a broad tropical-temperate transition zone from north to south, between approximately Shark Bay in the North, and Cape Leeuwin in the south (Morgan and

Wells, 1991). Despite the unusual current systems present off south-west Australia, there has been relatively little research on the regional biological oceanography. Until recently, the response of planktonic communities to physical and climatic forcing in the region has been virtually unknown.

1.2 The Strategic Research Fund for the Marine Environment (SRFME): Biological Oceanography Project

The SRFME Biophysical Oceanography project, initiated in 2002, aimed to investigate the oceanographic, hydro-chemical and biological dynamics of the coastal, shelf and offshore zones off south-western Australia (Koslow *et al.*, 2005). This was achieved by sampling for a period of three years (2.5 years for fish larvae), along a transect extending from the coast, out across the continental shelf and slope. The research involved six core research components:

- The physical structure and nutrient dynamics within the water column,
- Phytoplankton community composition, biomass and productivity,
- Microzooplankton communities and their grazing dynamics,
- Mesozooplankton communities and their grazing dynamics,
- Spatial structure of zooplankton communities,
- Larval fish (ichthyoplankton) assemblages and ecology.

The SRFME larval fish project aimed to document the larval fish assemblage structure along a fixed transect (the SRFME Biophysical Oceanography Two Rocks transect), from inshore, shelf and offshore waters off south-western Australia, and the variation in this structure between seasons, and between years. The project also intended to link temporal and spatial variability in larval fish assemblages to water

mass structure at the time of sampling, as well as other physical, biological and meteorological processes, in order to elucidate major influences on assemblage structure. An opportunistic study of larval fish assemblages within two mesoscale Leeuwin Current eddies was also completed, and aimed to explore the horizontal and vertical structure of assemblages in relation to the biophysical characteristics of the eddies.

1.3 The influence of physical and biological conditions on ichthyoplankton assemblages

The life cycles of most fish species include a planktonic larval phase, usually lasting from weeks to months (Brothers *et al.,* 1983; Moser and Boehlert, 1991). Mortality during this period is high, with typically less than one percent of offspring surviving through metamorphosis to settle in nursery or adult habitats (Houde, 1987; Chambers and Trippel, 1997). Variability in the mortality rates of larvae can have a disproportionately large influence on recruitment to the adult populations (Bailey, 1981).

Larval fish are influenced by a variety of physical and biological factors, operating at a range of temporal and spatial scales. However, the influences of such variables are not uniform among larval fish of different species. Species may have different life cycles, and various larval adaptations and characteristics; therefore, they react in different ways to their environment, and to changes in this environment (Leis, 1993; Marancik *et al.,* 2005). As a result, it is usually insightful to consider the entire larval fish assemblage within a study area, rather than just the abundances of one particular target species. The temporal and spatial variation of the larval fish assemblage at a

particular location may therefore be used as a multivariate measure of the reaction of fish larvae of different species to their immediate environment. The dynamics of a larval fish assemblage are best understood when considered in conjunction with data on the prevailing physical and biological conditions; in particular, those which affect larval fish feeding, survival and transport. Larval fish assemblages may also be useful in baseline studies of a region, as they tend to characterize the nature and variability of the biophysical environment.

Different physical oceanographic processes influence the distribution of larval fish on a variety of scales, ranging from a few metres to thousands of kilometres, therefore, larval distribution is likely to be determined by their interaction with a number of concurrent features (Bruce *et al.,* 2001; Hare *et al*., 2002). Larval ontogeny, behaviour and environmental conditions determine dispersal strategies, including when and how far to disperse (Urho, 1999). Dispersal strategies differ among species and between geographical regions, with some larvae being dispersed over large distances, and others being retained close to the nursery or adult habitats. However, as the eventual return of spawning products into the juvenile nursery area or adult habitat is a pre-requisite for the survival of the population, each species must utilize mechanisms for larval transport that enable some larvae to return, regardless of their distance travelled (Leis and Miller, 1976; Heath, 1992). Larvae may therefore employ predictable, recurrent oceanographic features and behaviours to ensure their dispersal to, or retention in, areas suitable for their feeding, growth and subsequent return (Urho, 1999). Spawning times may be shown to coincide with favourable dispersion processes, and to avoid times of unfavourable dispersion (Bakun, 1985; Olivar and Shelton, 1993). The geographical locations, and times, of adult fish spawning often

represent an evolutionary adaptation to the climatological mean water circulation pattern (Bakun, 1985), as the major life history characteristics such as spawning, migration, recruitment and feeding patterns of many species have evolved under the influence of current systems (Lenanton *et al.,* 1991; Hutchings *et al.,* 2002). Fluctuations in adult fish populations may therefore be affected by the location and velocity of such oceanographic features and transport mechanisms (Iles and Sinclair, 1982; Heath, 1992). As the importance of oceanographic features to larval fish distribution and survival has been realised, numerous studies on these topics have been conducted, covering most of the world's coastal oceans (e.g., Moser and Smith, 1993; Olivar and Shelton, 1993; Grothues and Cowen, 1999; Hare *et al.,* 2001).

Entrainment in large ocean currents, eddies and jets can result in the dispersal of larval fish eggs and larvae over potentially large areas of ocean. Larvae can be advected thousands of kilometres, to areas with different physical and biological conditions to those from near where they were spawned (Bailey, 1981; Houde, 1987; Nishimoto and Washburn, 2002). Mesoscale eddies, in particular, are commonly found in association with major current systems, including the California Bight (Logerwell *et al*., 2001), the Agulhas Current (Lutjeharms *et al*., 2003; Quartly and Srokosz, 2004), the Eastern Australian Current (Nilsson and Cresswell, 1981), and in the southeastern Indian Ocean (Morrow *et al*., 2003; Cresswell and Griffin, 2004). As eddies and jets form, they may entrain water from the continental shelf, and thus represent a significant means of offshore dispersion of continental shelf primary productivity, and fish larvae (Kasai *et al*., 2002; Fang and Morrow, 2003). However, the extent to which the entrainment of larval fish in these features affects their survival, and eventual recruitment to a parent population depends on both the

responses of larvae to such features, and their capabilities to determine their destination (Cowen, 2002).

The strength and flow direction of ocean currents are usually variable with depth through the water column (Heath, 1992). Fish larvae located at different depths in the same location will therefore be subject to different transport processes. Differences in vertical distributions can thus result in different spatial distributions for larvae spawned in the same place, and, if larvae can exploit the vertical structure of the water column, then the extent to which they can influence their dispersal will be substantially increased (Armsworth, 2001; Marancik *et al.,* 2005). Larval fish predator and prey concentrations may also differ with depth through the water column, resulting in different conditions for feeding and growth at different depths (Heath, 1992, Gray and Kingsford, 2003). Active depth selection by fish larvae may be advantageous by allowing larvae to align with depths of both favourable retention conditions, and favourable prey or predator concentrations (Heath, 1992). The suitability of particular depths and conditions will vary between different species (Leis, 1982; Cowen *et al*., 2003).

It is important to note that larval fish dispersal processes may not be limited to the transport of eggs and larvae by diffusion and/or advection (Heath, 1992). While passive advection is important to the dispersal of many larval fish, the interpretation of larvae as "passive particles" conflicts with numerous observations of larval fish behaviour (Cowen *et al*., 1993; Smith, 2000; Fisher, 2005). At larger spatial scales (e.g., between water masses), larval fish distributions appear to conform to hydrographic boundaries, in the character of passive particles (Olivar and Beckley,

1994). At smaller spatial scales (e.g., within water masses), larval behaviour appears to modify their distributions (Leis and Carson-Ewart, 1998; Kingsford *et al.,* 2002). Larvae may migrate vertically in the water column to take advantage of different currents and conditions at different water depths, thus affecting their horizontal transport (Grioche *et al*., 2000; Fisher and Bellwood, 2002). Later-stage larvae may also display strong swimming behaviour, and be capable of travelling at greater speeds than the ambient currents (Leis *et al*., 1996; Armsworth, 2001). Behaviours have been shown to differ among species in the same regional area (Cowen *et al*., 1993; Leis and Carson-Ewart, 1998).

Physical processes affect both the transport of fish larvae, and the biological characteristics of their environment. Ocean currents may transport larvae into areas with high or low concentrations of both food and potential predators (Simpson, 1987). Physical processes not only affect the magnitude of the plankton biomass, but also the species composition (Huntsman *et al*., 1981), which may, in turn affect larval fish feeding and survival (Lasker, 1975; Simpson, 1987). Wind-driven upwelling processes, for example, may influence larval fish transport by the advection of water offshore, and larval fish feeding and growth by the enrichment of surface nutrients, phytoplankton, and, consequently, secondary production (Hutchings *et al.,* 1995; Cudaback and Largier, 2001; Bjork and Nordberg, 2003). More extreme wind events, i.e., storms, can affect the spatial distribution of eggs and larvae, as well as that of their food and predators, by enhancing onshore transport and causing local vertical entrainment of water at the base of the mixed layer (Simpson, 1987). Storms may increase local primary production by entraining nutrients into the mixed layer, but may also destroy food patches, and disrupt discrete chlorophyll maximum layers,

resulting in insufficient food for some larvae and higher rates of starvation (Lasker, 1975; Maillet and Checkley, 1991).

Climatic cycles, such as El Niño, are a major influence on the strength and position of oceanographic features, on wind fields, and on other meteorological conditions (Tsai *et al.,* 1997; Sanchez-Velasco *et al.,* 2002). They therefore have a strong influence on fish recruitment, especially through their influence on larval fish transport and survival (e.g., Cubillos and Arcos, 2002; Funes-Rodriguez *et al*., 2001; Sanchez-Velasco *et al*., 2002; Tsai *et al.,* 1997). It is not always clear however, whether the effects on larvae are primarily due to transport issues, such as variations in the strength of major currents, and changes in regional hydrography, or with the changes in the biological environment associated with the observed shifts in sea surface temperature and consequent changes to the local plankton. Populations of small pelagic species, such as *Sardinops sagax* (Clupeidae), and *Engraulis* spp. (Engraulidae) are particularly variable in response to climatic and environmental cycles (Cubillos and Arcos, 2002; Hutchings *et al.*, 2002; Coombs *et al*., 2003, Smith and Moser, 2003). This variability in population sizes existed well before any significant human exploitation of these fish stocks, and can make fisheries based on them difficult to manage (Baumgartner *et al.*, 1992). Studies of the larvae of these species have therefore been used to examine the effects of environmental variability on recruitment to adult populations.

Patterns in larval fish assemblages may therefore be affected by a variety of physical and biological factors, operating over a wide range of temporal and spatial scales. However, the scale at which larval fish assemblages are studied will affect the

processes that are ultimately deemed to be important. Potentially influential physical and biological factors may vary in time as well as space, therefore recent meteorological and oceanographic events, as well as regional seasonal and climatic cycles may also be significant.

Larger scale studies have concluded that climate effects, such as El Niño were influential (Funes-Rodriguez *et al*., 2001), while others cite water mass history (Cowen *et al.*, 1993), and oceanographic processes such as upwelling (Olivar and Shelton, 1993), advection (Franco-Gordo *et al.*, 2001) and current position and strength (Hare *et al*., 2001; Hsieh *et al.,* 2005) to be most important in structuring larval fish assemblages. Assemblages may also be affected by finer-scale oceanographic features such as hydrographic fronts (Moser and Smith, 1993; Sabates *et al*., 2004), and local variations in temperature, salinity or chlorophyll biomass concentration (Groiche *et al*., 1999; Espinosa-Fuentes and Flores-Coto, 2004). Analysing oceanographic and environmental conditions at a finer scale still, some authors have emphasized the role of water column stability and stratification, and prey item patchiness in larval fish distribution (Lasker, 1975; Richardson *et al*., 1998). Some potentially important processes operate at the scale of the larvae themselves, such as small-scale turbulence, and its effect on prey encounter rates (Mackenzie, 2000), and predation rates on larvae (Bailey and Houde, 1989). Therefore, the perceived main influences on larval fish assemblage structure may vary according to the study location, the time of year, and the scale at which a study is conducted.

1.4 Thesis outline

This thesis examines the spatial and temporal structure of the larval fish assemblages along a transect across the continental shelf and slope off south-western Australia. Chapter 2 covers the taxonomic composition of larval fish assemblages, and relates them to the dominant oceanographic processes and water masses. Chapter 3 further explores the links between larval fish assemblage structure and various environmental variables, including biological, physicochemical, and meteorological parameters. A detailed examination of patterns of abundance for clupeiform larvae is presented in Chapter 4, including relation to environmental variables, and reproductive cycles. Chapter 5 compares the vertical and horizontal structure of larval fish assemblages between summer and winter sampling cruises, and relates assemblage patterns to regional oceanographic and biological processes. Chapter 6 contains a separate study, describing the larval fish assemblages in two mesoscale eddies of the Leeuwin Current, the results of which are from a multi-disciplinary research cruise that was carried out in October 2003. Finally, Chapter 7 discusses the overall conclusions of these investigations on larval fish assemblages of south-western Australia, as well as some suggested directions for future research.

Chapter 2: Neritic larval fish assemblages off south-western Australia in relation to water mass structure

2.1 Introduction

Many comprehensive larval fish assemblage studies have been undertaken world-wide (e.g., Olivar and Shelton, 1993; Gray and Miskiewicz, 2000; Hare *et al.*, 2001), but there has been very little research on assemblages in the south-east Indian Ocean, off south-western Australia. Most published work from Western Australia has, thus far, been restricted to studies on estuaries and the nearshore environment (e.g., Gaughan *et al*., 1990; Neira and Potter, 1992), with no comprehensive documentation of larval fish assemblages in continental shelf, slope and offshore waters. Baseline data on larval fish assemblage structure in these waters is of interest both from a fisheries management perspective, and also because of the unique oceanography of the region.

Whilst correlations between variation in the strength of the Leeuwin Current and the recruitment of some species to fisheries have been described (Lenanton *et al*., 1991; Caputi *et al*., 1996), the specific mechanisms responsible for these correlations are not well known. In particular, there have been no published studies incorporating both oceanographic data, and *in situ* collection of larval fishes. The work described here aimed to document larval fish assemblage structure in inshore, shelf and offshore waters across a transect located north of Perth, over a period of two and a half years. Spatial variation in assemblages, and seasonal and interannual patterns were determined, and related to dominant oceanographic processes and water masses. It was hypothesized that the seasonal and spatial structure of larval fish assemblages would reflect the seasonal and spatial structure of regional oceanographic processes.

2.2 Materials and methods

2.2.1 Study area and data collection

Sampling for this study was carried out along an 84km transect, located offshore of the town of Two Rocks (-31.52°S, 115.60°E) in Western Australia (Figure 2.1).

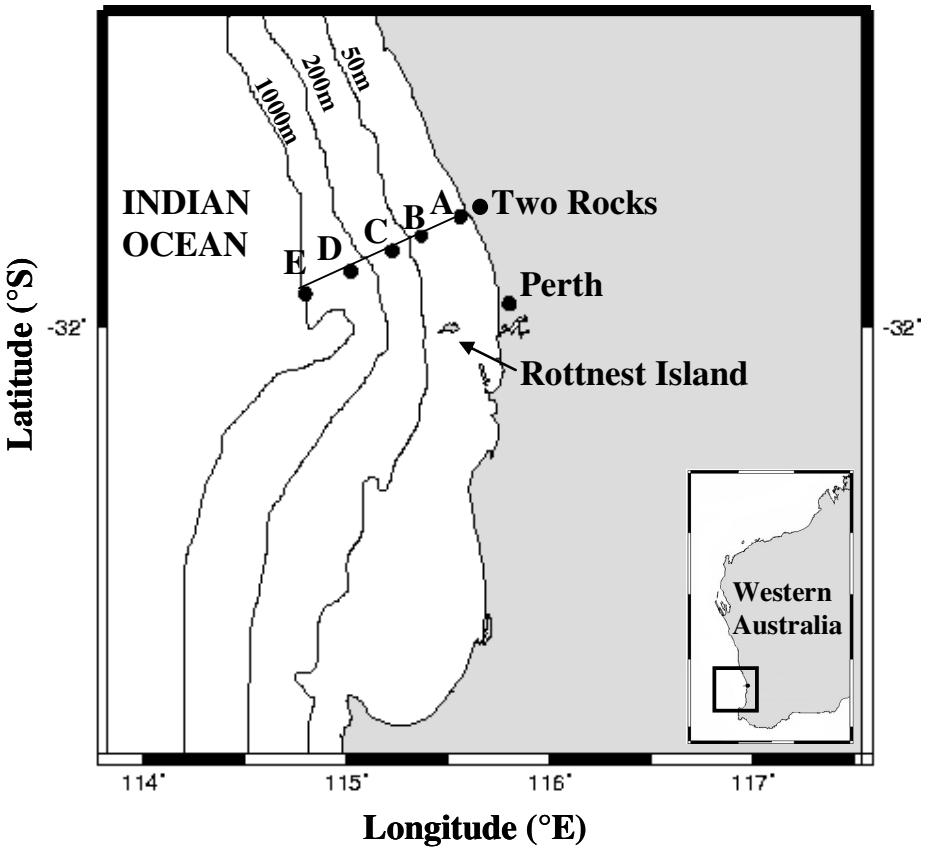

Figure 2.1: Study area off south-western Australia, showing stations sampled along the Two Rocks transect, August 2002 to December 2004. Figure adapted from Online Map Creation.

Five sampling stations (A - 18m depth, B - 40m, C - 100m, D - 300m, E - 1000m), were sampled along the transect line. Stations were chosen to represent coastal (A), inner shelf (B), outer shelf (C), shelf break (D) and offshore (E) environments. The program involved sampling for a period of two and a half years, August 2002 to

December 2004. All stations were sampled on a quarterly basis, and, in addition, the three inshore stations were sampled monthly, where possible (Table 2.1).

Table 2.1: Plankton and CTD sampling program on the Two Rocks transect, August 2002 to December 2004, indicating research vessels used, and stations sampled.

Cruise Number	Cruise start date	Vessel	Stations Occupied
04_02	17/08/2002	*RV Naturaliste*	A - E
06_02	17/12/2002	*RV Naturaliste*	A – E
01_03	27/01/2003	*Mesocat*	A
02_03	08/02/2003	*RV Naturaliste*	A – E
03_03	02/04/2003	*Mesocat*	A – C
04_03	28/04/2003	*RV Naturaliste*	A – E
05_03	09/06/2003	*Mesocat*	A – C
06_03	01/08/2003	*Mesocat*	A
07_03	23/08/2003	*RV Southern Surveyor*	A – E
08_03	26/08/2003	*Mesocat*	A – C
09_03	24/10/2003	*RV Southern Surveyor*	A – E
10_03	08/11/2003	*RV Southern Surveyor*	A – E
11_03	01/12/2003	*RV Naturaliste*	A – E
01_04	20/01/2004	*RV Southern Surveyor*	A – E
02_04	07/04/2004	*Mesocat*	A – C
03_04	19/04/2004	*Maritime Image*	A, D-E
04_04	25/06/2004	*Mesocat*	A – C
05_04	18/07/2004	*Maritime Image*	A – E
06_04	18/08/2004	*Mesocat*	A, C
07_04	20/09/2004	*RV Naturaliste*	A – E
08_04	28/10/2004	*Mesocat*	A – C
09_04	24/11/2004	*Mesocat*	A – C
10_04	15/12/2004	*RV Naturaliste*	A – E

Vertical CTD (conductivity-temperature-depth) casts were completed using a Seabird Model SBE 19+ instrument at all stations where larval fish were sampled (Koslow *et al.*, 2005). Temperature and salinity were measured approximately four times per metre through the water column, with data later binned every metre, using standard Seabird software. Casts were to 300m depth, or to just above the bottom in shallower water. Temperature and salinity measurements through the water column at each station were used to characterise water masses. Chlorophyll *a* biomass data (mg/m^3) were derived from correlations to fluorescence data (volts), which were taken from a fluorometer attached to the CTD (Koslow *et al*., 2005).

Sea-surface temperature satellite images were derived from the advanced, very high resolution radiometer (AVHRR). These images were available for all cruises except two (August and November 2004), and were also used to determine surface water mass structure on each sampling occasion. Satellite SST images (and images used hereafter) used Band 4 only, and were therefore brightness temperatures only, not true sea surface temperature. This resulted in the under-estimation of actual sea-surface temperature from each image, but allowed a clearer interpretation of the current structure, as brightness images are less noisy than true SST images (A. Pearce, CSIRO, *pers. comm.* 2006). Sea-surface temperature data were acquired from the Western Australian Satellite Technology and Applications Consortium (WASTAC), and the images were processed by CSIRO Marine Research at Floreat, Western Australia.

Plankton samples were taken with day-time oblique bongo net tows to 150m depth, or just above the bottom in shallower water. Nets were fitted with both 100μm and

355µm mesh (mouth area 0.196m^2, diameter 0.5m), and were towed at about 2 knots. The 355µm net was fitted with a General Oceanics flowmeter. All tows were replicated, with the exception of stations A - C on the November 2002 cruise, station C on the March and June 2003, and November 2004 cruises, and station B on the October 2003 and October 2004 cruises. Plankton samples from the first replicate tow were split immediately after collection, with half the sample fixed in 10% buffered formaldehyde, and half in 100% ethanol, to allow for later analyses on genetics and/or larval fish otoliths. Samples preserved in ethanol had the ethanol replaced after 24 hours to ensure proper preservation. Samples from the second replicate tow were preserved in formaldehyde only. A dissecting microscope was used to remove larval fish from the 355µm bongo net samples. Larvae were then preserved in 70% ethanol, and identified to family, and species where possible, using relevant literature (e.g., Moser *et al*., 1984; Neira *et al*., 1998; Leis and Carson-Ewart, 2000; Richards *et al*., 2006a).

2.2.2 Data analyses

Stations were classified as being located within one of five water masses: summer inshore water, winter inshore water, Leeuwin Current, Capes Current or Sub-tropical Surface Water (STSW) (Woo *et al*., submitted; Pearce *et al*., in press). In the rare case that two water masses appeared to be present at a station (one on top of the other), the surface water mass was used, most larval fish were found in the upper water column (see Chapter 5). Where the satellite image appeared to show a different water mass over a station to the measured TS data, the TS data were taken as the more accurate representation. This occurred on four occasions: February 2003 station C, March 2003 station C, June 2003 station A and June 2004 station A. The TS characteristics of the

water masses in the study area have been shown to overlap when data from throughout the year is considered (Gersbach *et al*., 1999; Woo, *et al*., submitted), largely due to the Leeuwin Current cooling, and increasing in salinity as it flows southward (Cresswell, 1991). However, water masses are still generally easily definable on a cruise by cruise basis (Hanson *et al*., 2005; Woo *et al*., submitted), and in this study, they were defined by their relative characteristics within a season, and differences to adjacent water masses. Summer inshore water was defined as the water mass present next to the coast in summer, and was warmer and more saline than adjacent Capes Current water. Winter inshore water was defined as the water mass next to the coast in winter, colder than the adjacent Leeuwin Current, and with higher salinity. The Leeuwin Current was further distinguished from the Capes Current by its higher temperature, and lower salinity. STSW was found offshore of the Leeuwin Current, and was easily distinguished from Leeuwin Current water by its lower temperature. Averaged data from the top five metres of the water column only was used in the display of TS envelopes, to aid clarity and interpretation.

From the flowmeter data, the volume of water sampled in each plankton tow was calculated, allowing the expression of larval fish numbers per cubic metre of seawater (i.e., concentrations). Where replicate bongo tows existed, mean concentrations and standard errors were calculated. Two-way analysis of variance (ANOVA) in SPSS for Windows 14.0 was used to test for the presence of significant differences between mean larval fish concentrations between sampling stations, and between seasons, with Tukey's post-hoc test used for pairwise comparisons. The presence of an interaction effect between water depth and season was also tested for.

Larval fish assemblage structure was investigated using the Primer-6 software package (Clarke and Warwick, 2005). To reduce the weighting of dominant species, species concentration values were log transformed (log_{x+1}) prior to analysis. The appropriate transformation was determined by prior examination of the relationship between the mean and standard deviation of replicated samples (Clarke and Warwick, 2001). A triangular similarity matrix based on Bray-Curtis similarities was created first, which compared the similarity of all samples with each other. An hierarchical, agglomerative dendrogram was created from the similarity matrix, using group average linkages, with non-metric Multi-Dimensional Scaling (MDS) ordination used to display the similarities between stations in two-dimensional space. The significance of the cluster groups created was tested by similarity profile (SIMPROF) analysis. This sub-routine calculates the similarities between samples, and then plots them against their rank, to give a similarity profile. Permutation testing was used to determine whether the structure within cluster groups was statistically different from a random result. This process randomly re-labelled samples, and repeated the SIMPROF procedure 999 times to produce a 95% upper and lower envelope of the simulated profiles, which were then compared to the actual result. This procedure therefore determined where there was no significant sub-group structure within cluster groups, i.e., the point at which the further splitting of cluster groups of samples became spurious (Clarke and Warwick, 2001). This analysis resulted in the characterisation of discrete, significant larval fish assemblage groups, which were given names to reflect when, and where, their constituent samples were collected.

The analysis of similarity (ANOSIM) sub-routine (Clarke and Warwick, 2005) was used to test the null hypothesis of no difference in larval assemblages between the five

stations along the transect. This procedure compared the average rank similarities within the pre-defined groups of samples with the average similarity between groups. R-values close to 1 indicated a strong separation between groups, while an R-value of 0 indicated no differences between groups (Clarke and Warwick, 2001). The significance of the result obtained was determined using permutation testing. A result was determined to be statistically significant if the significance value was <5%. Assemblage data were allocated into four seasons, following the traditional southern hemisphere divisions as follows: summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Differences in larval fish assemblages between seasons, and between different water masses, were tested for, also using the ANOSIM procedure. Each ANOSIM test produced both a global R statistic, and pairwise comparisons between the pre-defined groups.

Lastly, the similarity percentage routine SIMPER (Clarke and Warwick, 2005) was applied to the data to identify species characteristic of each larval fish assemblage from the SIMPROF analyses, and also those species responsible for distinguishing assemblages. Taxa which characterised larval fish assemblages were identified using a ratio of the mean contribution of any one species to the overall similarity within samples groups ($\overline{\delta}_i$), to the standard deviation of $\overline{\delta}_i$ values from all constituent species [SD($\overline{\delta}_i$)]. Species where [$\overline{\delta}_i$ /SD($\overline{\delta}_i$)] was greater than 1.4 were considered to be good characterising species (Clarke and Warwick, 2001). The same ratio was used to identify species useful for discriminating between assemblage groups, with the mean contribution of any one species to the overall dissimilarity between sample groups considered in the same way.

2.3 Results

2.3.1 Oceanographic conditions

Oceanographic conditions during the two and a half years of sampling showed a strong seasonal pattern (Koslow *et al.*, 2005). During autumn and winter, the Leeuwin Current flowed strongly southwards along the shelf break, occasionally breaking into seawards meanders and eddies, or intruding shorewards across the shelf, at times nearly reaching the coast (Figure 2.2).

During spring, the onset of strong southerly winds weakened the Leeuwin Current and initiated the Capes Current, which flowed northwards past the study area, occasionally inducing a small wake to the north of Rottnest Island. This pattern continued through the summer months, until the strengthening of the Leeuwin Current again in autumn. The strength and location of these features varied under the influence of local and regional climatic conditions (Pearce *et al*., in press). Their effect on the study transect therefore varied through space and time, so that oceanographic conditions at the same time between years were not necessarily identical.

A TS envelope was calculated for each of the five water masses sampled, using averaged data from the top five metres of the water column only (Figure 2.3). At station A, three water masses were found: summer inshore water, winter inshore water and Leeuwin Current (on two occasions only). Summer inshore water was generally warmer (>18°C) and more saline (>35.5) than both winter inshore water, and Leeuwin Current water, although the envelopes for each water mass showed significant overlap.

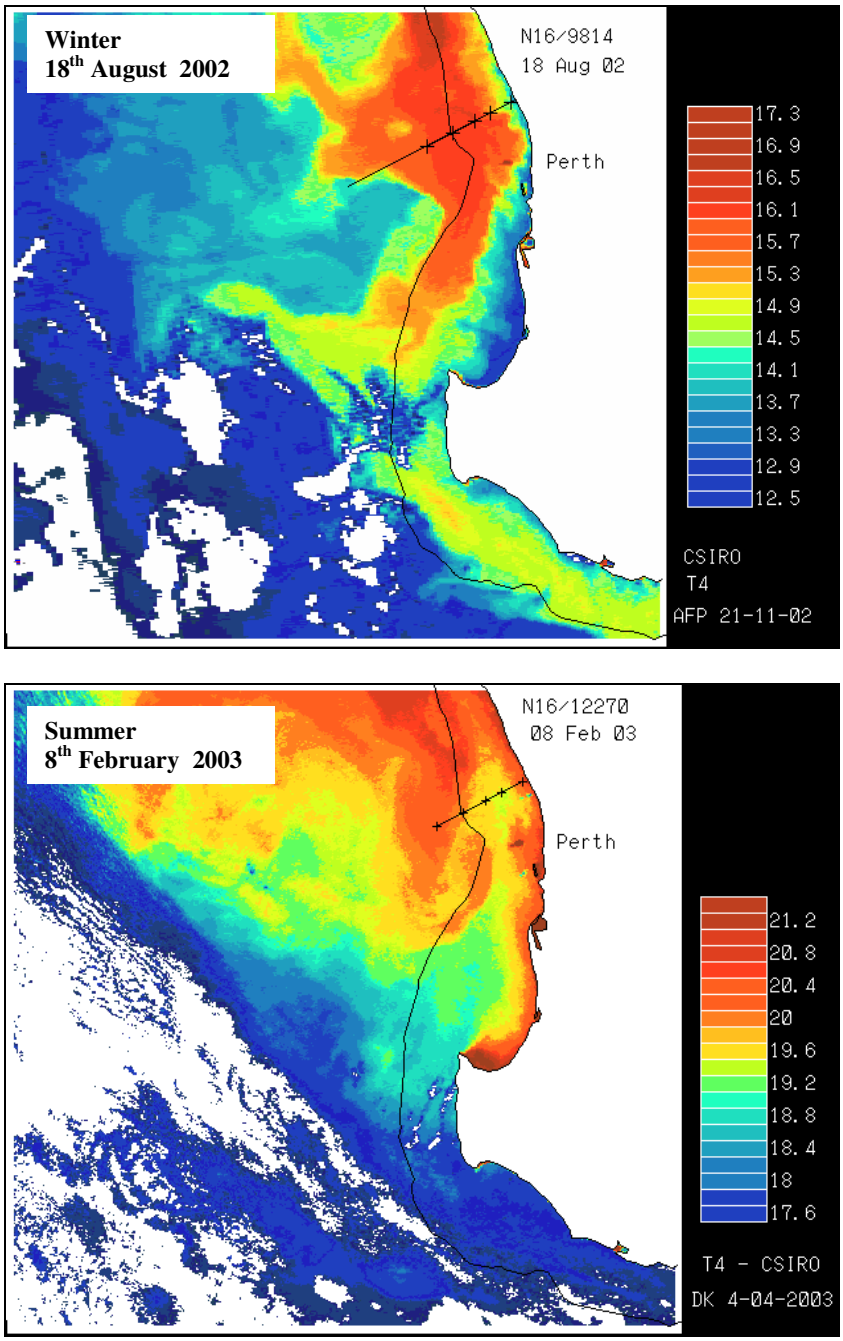

Figure 2.2: Sea-surface temperature satellite images of the Leeuwin and Capes Currents during a winter and a summer oceanographic regime off south-western Australia (Band 4 only). Note different colour and temperature scales between images. Source: A. Pearce, WASTAC.

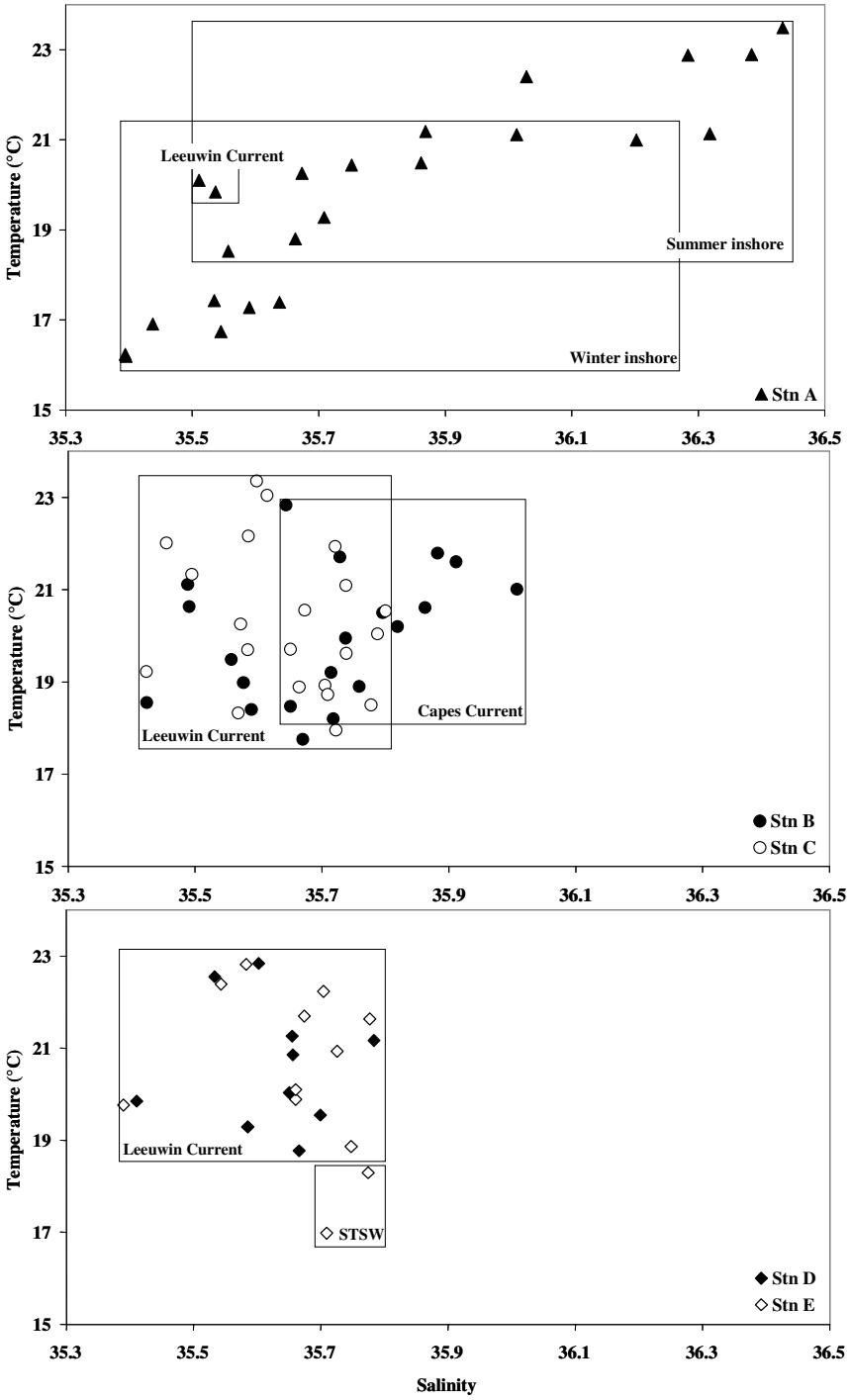

Figure 2.3: Temperature and salinity (TS) envelopes for water masses present at inshore (station A), shelf (stations B and C) and offshore (stations D and E) sampling stations across the Two Rocks transect, August 2002 to December 2004. STSW = Sub-tropical Surface Water.

On the continental shelf (stations B and C combined), two water masses were present: the Capes Current (mostly in summer, and more often at station B), and the Leeuwin Current (Figure 2.3). The Capes Current was generally more saline (>35.6) than the Leeuwin Current, although, as with the inshore station, there was significant overlap between the characteristics of the two water masses. Determination of water mass structure at these stations, at any particular point in time was therefore a relative exercise, with differences between the physical characteristics of water masses not consistent through all seasons.

The offshore stations (stations D and E combined), were predominantly located within the Leeuwin Current, although station E was located in STSW on two occasions (Figure 2.3). This water mass was distinguishable from the Leeuwin Current by lower sea surface temperatures in the former (<18.5°C).

The determination of the water mass present at each station showed that the same station sampled at the same time in different years was occasionally located within a different water mass (Table 2.2). For example, in December 2002, station C was located within the Leeuwin Current, while in December 2003 and 2004, this station was located within the Capes Current. Similarly, in October 2003, station C was located within the Leeuwin Current, while in October 2004, station C was under the influence of the Capes Current. In March 2003, station A was classified as being in summer inshore water, while in March 2004, station A was in winter inshore water. Offshore stations were less variable, although in August 2002, station E was in the Leeuwin Current, while in 2003, this station was located in STSW.

Temperature, salinity and chlorophyll biomass sections across the sampled transect taken during summer, autumn, winter and spring show the contrasting oceanographic conditions present between seasons (Figure 2.4). In summer, water temperatures across the transect were warm, especially inshore, and the water column was stratified for temperature, from shelf to offshore waters. Salinity was high inshore, with the Leeuwin Current present as a lower salinity water mass at the surface at stations D and E. Chlorophyll though the water column was generally low. In autumn, the water column was warm and well mixed, with high salinity water persisting inshore. Chlorophyll biomass on this particular cruise (April 2003) was low.

During winter, water temperatures were cooler inshore, with the Leeuwin Current visible as a warmer water mass located against the shelf. Salinity was lower than in summer or autumn, however, chlorophyll biomass was much higher. In early spring, water temperatures across the transect were similar to winter, but salinity was slightly higher, and chlorophyll biomass much lower, especially in surface waters (Figure 2.4).

Table 2.2: Water mass present at each station sampled on each cruise along the Two Rocks transect, August 2002 to December 2004. (Classification based on Woo *et al*., submitted; A. Pearce, CSIRO, *pers. comm*. 2005).

Cruise	Station	Water Mass	Cruise	Station	Water Mass
August 2002	A	Winter Inshore	**November 2003**	A	Summer Inshore
	B	Leeuwin Current		B	Capes Current
	C	Leeuwin Current		C	Capes Current
	D	Leeuwin Current		D	Leeuwin Current
	E	Leeuwin Current		E	Leeuwin Current
November 2002	A	Summer Inshore	**December 2003**	A	Summer Inshore
	B	Capes Current		B	Capes Current
	C	Capes Current		C	Capes Current
December 2002	A	Summer Inshore		D	Leeuwin Current
	B	Capes Current		E	Leeuwin Current
	C	Leeuwin Current	**January 2004**	A	Summer Inshore
	D	Leeuwin Current		B	Capes Current
	E	Leeuwin Current		C	Leeuwin Current
January 2003	A	Summer Inshore		D	Leeuwin Current
February 2003	A	Summer Inshore		E	Leeuwin Current
	B	Capes Current	**March 2004**	A	Winter Inshore
	C	Leeuwin Current		B	Capes Current
	D	Leeuwin Current		C	Leeuwin Current
	E	Leeuwin Current	**April 2004**	A	Winter Inshore
March 2003	A	Summer Inshore		D	Leeuwin Current
	B	Capes Current		E	Leeuwin Current
	C	Leeuwin Current	**June 2004**	A	Leeuwin Current
April 2003	A	Winter Inshore		B	Leeuwin Current
	B	Leeuwin Current		C	Leeuwin Current
	C	Leeuwin Current	**July 2004**	A	Winter Inshore
	D	Leeuwin Current		B	Leeuwin Current
	E	Leeuwin Current		C	Leeuwin Current
June 2003	A	Leeuwin Current		D	Leeuwin Current
	B	Leeuwin Current		E	Leeuwin Current
	C	Leeuwin Current	**August 2004**	A	Winter Inshore
July 2003	A	Winter Inshore		C	Leeuwin Current
August 2003	A	Winter Inshore	**September 2004**	A	Winter Inshore
	B	Leeuwin Current		B	Leeuwin Current
	C	Leeuwin Current		C	Leeuwin Current
	D	Leeuwin Current		D	Leeuwin Current
	E	STSW		E	STSW
September 2003	A	Winter Inshore	**October 2004**	A	Summer Inshore
	B	Leeuwin Current		B	Capes Current
	C	Leeuwin Current		C	Capes Current
October 2003	A	Summer Inshore	**November 2004**	A	Summer Inshore
	B	Capes Current		B	Capes Current
	C	Leeuwin Current		C	Capes Current
	D	Leeuwin Current	**December 2004**	A	Summer Inshore
	E	Leeuwin Current		B	Capes Current
				C	Capes Current
				D	Leeuwin Current
				E	Leeuwin Current

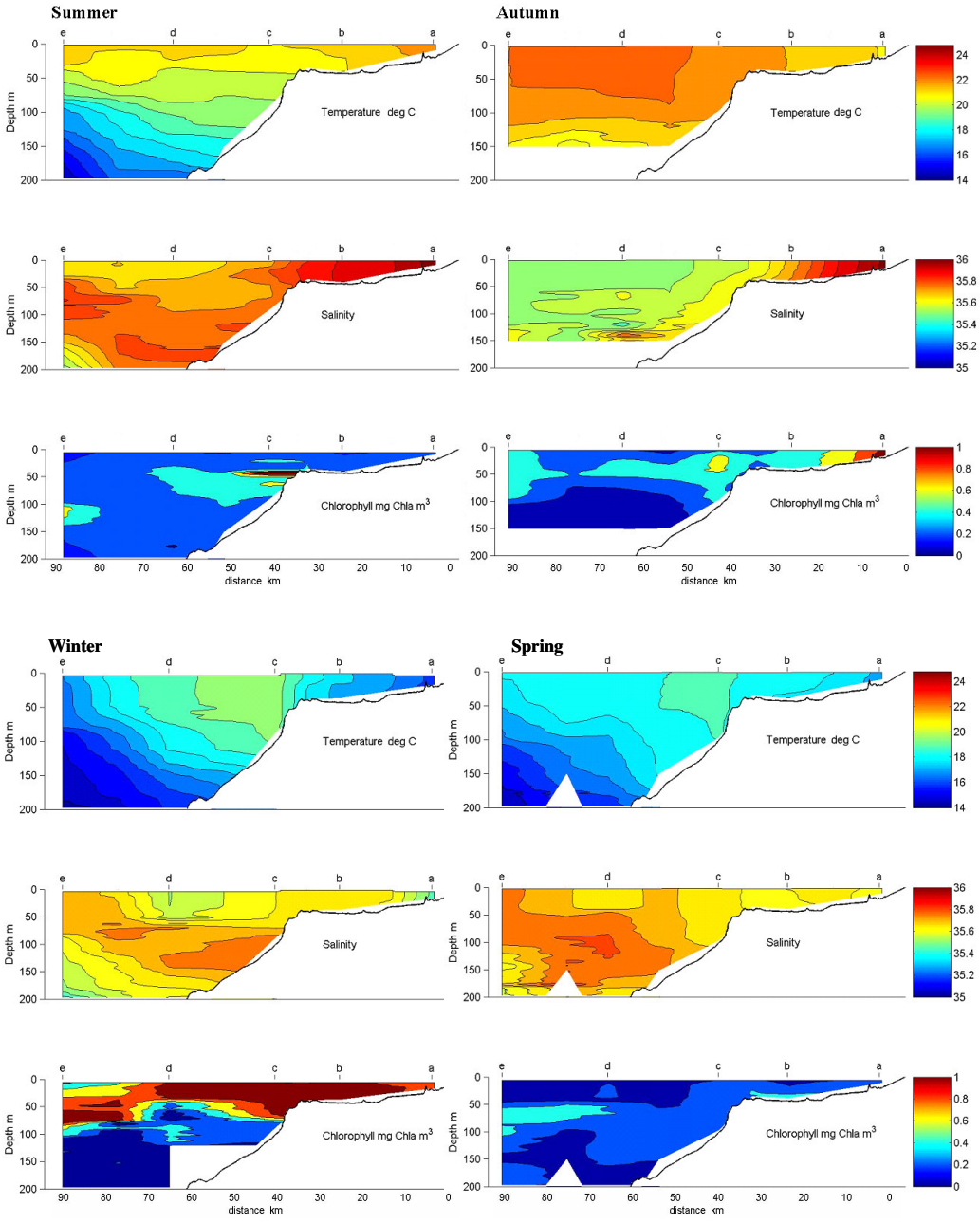

Figure 2.4: Representative temperature, salinity and chlorophyll sections along the Two Rocks transect, derived from CTD data. Months shown are December 2004 (summer), April 2003 (autumn), August 2003 (winter) and September 2004 (spring). Letters denote sampling station. Data supplied through the SRFME Biophysical Oceanography project, courtesy of Nick Mortimer (CSIRO Marine and Atmospheric Research).

2.3.2 Taxonomic composition of larval fish assemblages

A total of 24 865 fish larvae were identified from plankton samples collected over the study period, comprising 148 taxa from 93 families (Appendix 1). Taxa collected included those from inshore reef families, such as the Blenniidae, Gobiidae and Monacanthidae, as well as larvae of pelagic families, such as the Clupeidae, with *Sardinops sagax* and *Etrumeus teres* the most abundant species within this family. Oceanic fish larvae from the Myctophidae, such as *Diogenichthys atlanticus* and *Diaphus* "slender" spp., were abundant at offshore stations, with larvae from the Phosichthydae (mostly *Vinciguerria* spp.) and Gonostomatidae also found. Some tropical vagrant larvae such as *Chromis* sp. 1 (Pomacentridae) were collected, mostly from outer shelf stations during summer and autumn.

Determination of the percentage composition by family of larvae captured at each sampling station (A to E) revealed strong spatial separation in assemblages with water depth (Figure 2.5). Fish larvae from the Gobiidae (20%), Clinidae (16%) and Tripterygiidae (13%) were the most abundant inshore (Station A). On the shelf, (stations B and C), larvae from the Clupeidae were the most abundant (18% and 22%, respectively), followed by those from the Labridae (18% and 15%, respectively). However, station B assemblages contained a higher percentage of Engraulidae (9%) and Creedidae (7%) fish larvae than station C, while station C assemblages contained more larvae from the Myctophidae (14%), and Acropomatidae (4%). Offshore, at stations D and E, larval fish assemblages were dominated by species from the Myctophidae (57% and 58%, respectively). Fish larvae from the Phosichthydae (13% and 10%), and Gonostomatidae (3% and 7%) were also abundant at these stations.

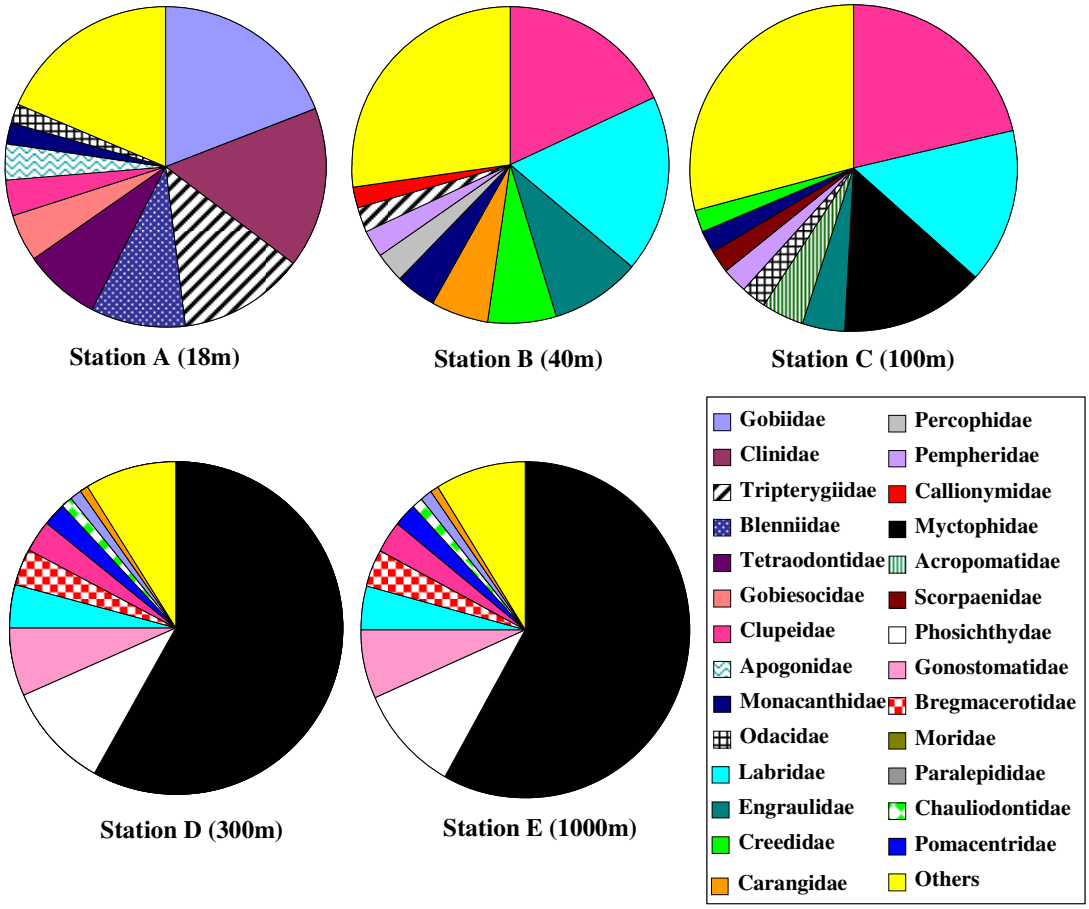

Figure 2.5: Percentage composition by family of the larval fishes found at sampling stations A to E along the Two Rocks transect, August 2002 to December 2004.

Larval fish concentrations were highly variable both spatially and temporally (Figure 2.6). Mean concentrations at station A were the most predictable with season, being highest in the summer months (up to a mean of 4.14 fish larvae/m^3 in December 2004), and lowest during winter (down to a mean of 0.06 fish larvae/m^3 in July 2004). Concentrations at stations B and C were more variable, with neither station showing significant differences in mean larval fish concentrations between seasons. There were very high mean concentrations in the last three months of 2004 (up to 7.43 fish larvae/m^3 at station B in October 2004). Stations D and E had lower, less variable mean concentrations, ranging from 0.03 fish larvae/m^3 in August 2003 to 0.73 fish larvae/m^3 in December 2003, both at station E.

A significant main effect was obtained for water depth ($p<0.001$), with station B supporting higher larval fish concentrations than station A ($p=0.01$), station D ($p<0.001$), or station E ($p<0.001$). Larval fish concentrations at station C were also higher than at stations D ($p=0.02$) or E ($p=0.01$). A significant main effect was also obtained for season ($p<0.001$), with higher mean larval fish concentrations found during summer than during autumn ($p=0.01$) or winter ($p<0.001$). Larval fish concentrations found during spring were also higher than those from winter ($p=0.01$).

There was no interaction effect between water depth and season ($p=0.14$), indicating that differences between water depths operated independent of season, and vice versa. Variability in larval fish concentration between replicate tows was generally low, with the two tows from January 2003 showing the greatest disparity in concentrations (SE = 1.79, or 65.3% of mean).

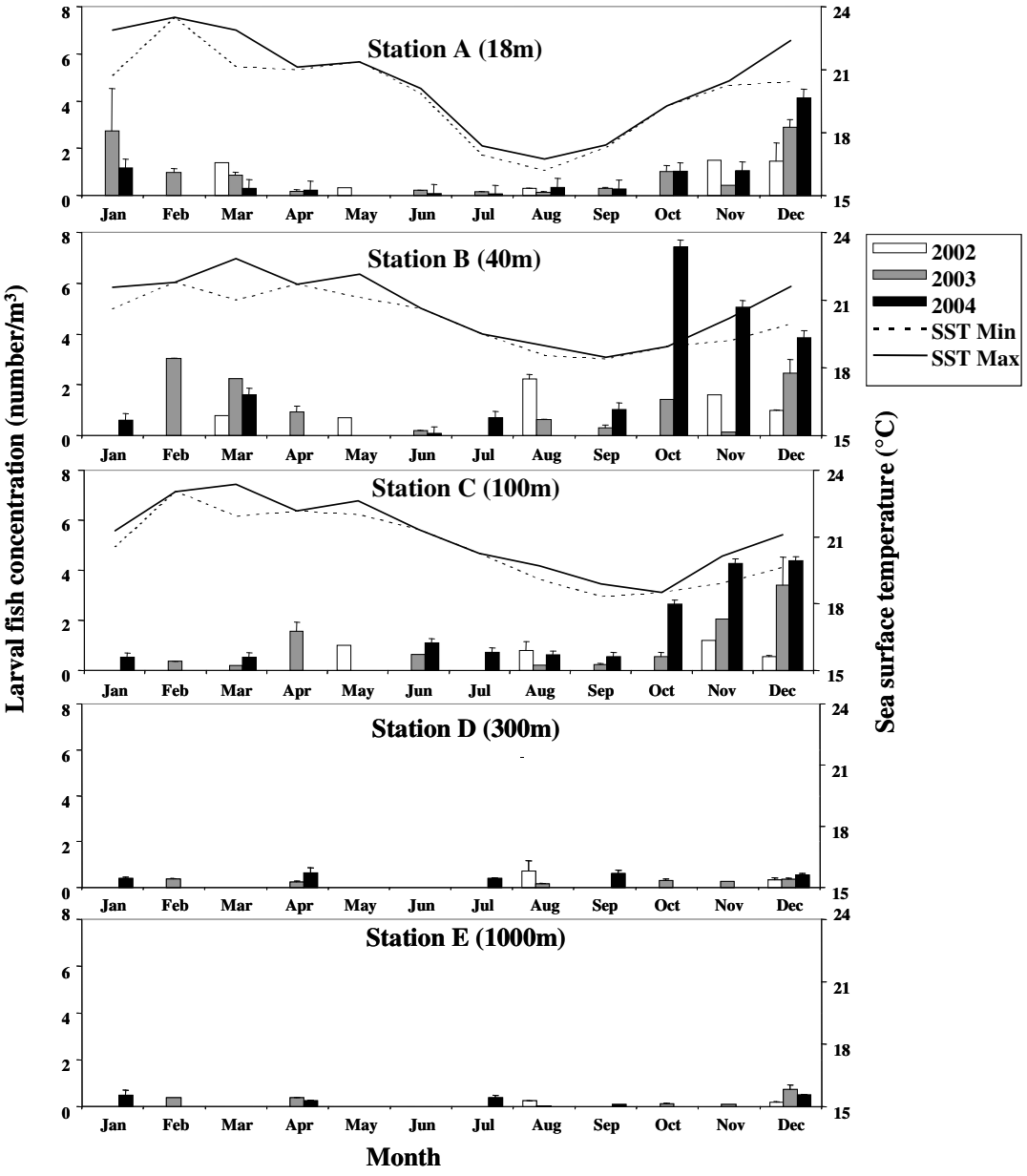

Figure 2.6: Mean concentration (number/m^3) of larval fish at stations A to E on the Two Rocks transect off south-western Australia, 2002 to 2004. SST minimum and maximum values from CTD data, for stations at which larval fish assemblages were sampled, are also shown for stations A to C. SST data from stations D and E was insufficient to show annual trends.

2.3.3 Larval fish assemblage structure

Comparison of assemblages between sampling stations, between seasons, and between water masses using ANOSIM revealed significant spatial and temporal differences. Assemblages at each station, averaged across seasons, were all significantly different to each other, with the exception of stations B and C (R=0.07), and stations D and E (R=-0.08) (Table 2.3). Differences were more pronounced with greater spatial separation of stations, as shown by the higher R-statistics for comparisons between stations further apart. Station A larval fish assemblages were the most distinctive.

Assemblages from each season, averaged across stations, were all significantly different from each other (Table 2.4), with assemblages from winter and summer the most distinct (R=0.53). Assemblages from summer and autumn, and spring and summer were the least distinct from each other (R=0.21 for each analysis).

Table 2.3: ANOSIM comparison of larval fish assemblages at each sampling station across the Two Rocks transect, averaged across seasons. Test statistics (R) are shown, with statistical significance of result in parentheses. ** denotes result significant at p<0.01

Stations compared	ANOSIM test result
A, B	R=0.69 (p=0.001**)
A, C	R=0.82 (p=0.001**)
A, D	R=0.94 (p=0.001**)
A, E	R=0.97 (p=0.001**)
B, C	R=0.07 (NS)
B, D	R=0.79 (p=0.001**)
B, E	R=0.86 (p=0.001**)
C, D	R=0.41 (p=0.001**)
C, E	R=0.50 (p=0.001**)
D, E	R=-0.08 (NS)

Table 2.4: ANOSIM comparison of larval fish assemblages by season, averaged across sampling stations across the Two Rocks transect. Test statistics (R) are shown, with statistical significance of result in parentheses. * denotes result significant at p<0.05, ** denotes result significant at p<0.01.

Seasons compared	ANOSIM test result
Winter, Spring	R=0.28 (p=0.002**)
Winter, Summer	R=0.53 (p=0.001**)
Winter, Autumn	R=0.30 (p=0.004**)
Spring, Summer	R=0.21 (p=0.005**)
Spring, Autumn	R=0.44 (p=0.001**)
Summer, Autumn	R=0.21 (p=0.01*)

The water mass present on each sampling occasion was the best descriptor of the larval fish assemblage present, with assemblages from different water masses all significantly and strongly distinct from each other, as shown by the high R-statistics (Table 2.5).

Table 2.5: ANOSIM comparison of larval fish assemblages by water mass along the Two Rocks transect. Test statistics (R) are shown, with statistical significance of result in parentheses. * denotes result significant at p<0.05, ** denotes result significant at p<0.01.

Water masses compared	ANOSIM test result
Winter Inshore, Leeuwin Current	R=0.75 (p=0.001**)
Winter Inshore, Summer Inshore	R=0.56 (p=0.002**)
Winter Inshore, Capes Current	R=0.88 (p=0.001**)
Winter Inshore, Sub-tropical Surface Water	R=0.99 (p=0.015*)
Leeuwin Current, Summer Inshore	R=0.79 (p=0.001**)
Leeuwin Current, Capes Current	R=0.53 (p=0.001**)
Leeuwin Current, Sub-tropical Surface Water	R=0.45 (p=0.013*)
Summer Inshore, Capes Current	R=0.70 (p=0.001**)
Summer Inshore, Sub-tropical Surface Water	R=1.00 (p=0.011*)
Capes Current, Sub-tropical Surface Water	R=0.99 (p=0.005**)

Assemblages from stations located within the summer inshore water mass, and those from stations within the Sub-Tropical Surface Water were the most distinct (R=1.00),

while assemblages from the Leeuwin Current versus those from the Sub-tropical Surface Water were the least distinct (R=0.45), but still significantly different from each other.

Multi-dimensional scaling (MDS) ordination of larval fish assemblages from all stations showed the clear separation of assemblages from station A, and the spatial progression in assemblage structure out to stations D and E (Figure 2.7A). Figure 2.7B shows the same MDS ordination presented in Figure 2.7A, with larval fish assemblages this time coded for the water mass present at each station at the time of sampling. The underlying influence of water mass in structuring larval fish assemblages is evident, although assemblages within the Leeuwin Current still showed spatial variation between inner shelf (station B) and offshore (station E) stations. The effect of inshore Leeuwin Current intrusions on the inshore larval fish assemblage is shown, with two station A samples taken when the Leeuwin Current extended inshore found to have assemblages more typical of inner shelf stations. These stations are circled in Figure 2.7A.

SIMPROF analysis of all of the larval fish data from all samples resulted in the characterisation of 12 assemblages, which were given names relating to where and when they were found. Three inshore assemblages (*winter inshore, summer inshore, autumn inshore*), five shelf assemblages (*mixed shelf, summer shelf, spring shelf, March inner shelf and autumn mid-shelf*) and four offshore assemblages (*mixed offshore, summer offshore, STSW and winter offshore*) were characterised (Table 2.6). The inshore assemblages were the most clearly structured by season, with some shelf and offshore assemblages also found only at a particular time of year (e.g., *summer*

shelf, *winter offshore*). Other shelf and offshore assemblages were not strongly associated with a particular time of year (e.g., *mixed shelf* assemblage).

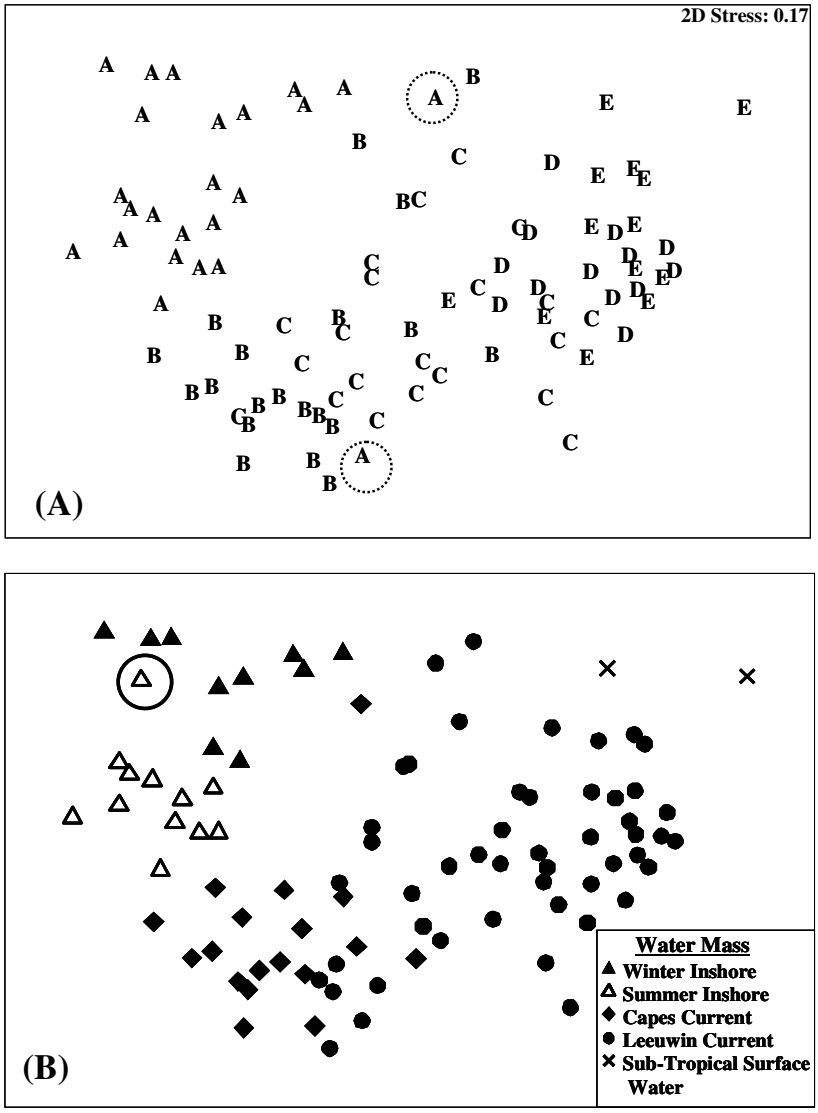

Figure 2.7: Multi-dimensional scaling (MDS) representation of larval fish assemblage structure for all stations across the Two Rocks transect, August 2002 to December 2004. Samples are coded by (A) sampling station and (B) water mass in which the sample was collected. Two station A samples taken within coastward Leeuwin Current intrusions are circled.

All assemblages were compared and characterised, to find the most common fish species present within each larval assemblage, and also those species whose presence tended to either consistently characterise, or consistently distinguish between assemblages. The March inner shelf and STSW assemblages were not included, as the comparative statistic $\overline{\delta}_i$ /SD($\overline{\delta}_i$) requires three samples or more for the calculation (Clarke and Warwick, 2001).

The *winter inshore* assemblage was a low concentration, low diversity assemblage, characterised by the presence of Clinidae sp. 1 larvae (77%) (Table 2.6), with *Alabes* sp. 1 (7%), and Monacanthidae spp. (4%) also common. In contrast, the *summer inshore* assemblage was a high concentration, high diversity assemblage, which was characterised by Clinidae sp. 1 (13%), and Tripterygiidae sp. 1 (13%). Gobiidae sp. 1 larvae (23%), and *Parablennius postoculomaculatus* (13%) were also common in this assemblage, but showed more variable concentrations between samples. The *summer inshore* assemblage was distinguished from the *winter inshore* assemblage by greater concentrations of Monacanthidae spp. larvae, and Clinidae sp. 1 in the former.

The *autumn inshore* assemblage was dominated by Tripterygiidae sp. 1 larvae (75%), with lower concentrations of Clinidae larvae (8%) and *Engraulis australis* (6%). The *autumn inshore* assemblage was distinguished from the *summer inshore* assemblage by lower concentrations of Monacanthidae spp., and from the *winter inshore* assemblage by its higher concentrations of Tripterygiidae sp. 1, and lower concentrations of Clinidae sp. 1, and *Alabes* sp.

Table 2.6: Larval fish assemblages from the Two Rocks transect determined by SIMPROF analysis, with constituent samples shown by month, year and station.

Assemblage	Summer	Autumn	Winter	Spring	Characteristic species (from SIMPER analysis)
Inshore assemblages					
Winter Inshore			August 02_A July 03_A August 03_A July 04_A August 04_A	September 03_A November 03_A September 04_A	Clinidae sp. 1
Summer Inshore	December 02_A January 03_A February 03_A December 03_A January 04_A December 04_A	March 03_A		November 02_A October 03_A October 04_A November 04_A	Clinidae sp. 1 Tripterygiidae sp. 1
Autumn Inshore		April 03_A March 04_A April 04_A			Tripterygiidae sp. 1
Shelf assemblages					
Mixed Shelf	December 02_B January 04_B January 04_C	April 03_B April 03_C	August 02_B August 02_C August 03_B June 03_A June 03_B June 03_C	October 04_C	*Sardinops sagax*
Summer shelf	February 03_B December 03_B December 03_C December 04_B December 04_C			November 02_B October 03_B November 03_C October 04_B November 04_B November 04_C	Labridae sp. 1
Spring Shelf	December 02_C December 03_E			November 02_C September 03_B September 03_C October 03_C November 03_B September 04_B	Labridae sp. 1 *Sardinops sagax*
March Inner Shelf		March 03_B March 04_B			Not enough samples to calculate
Autumn Mid-shelf		March 03_C	June 04_A June 04_B		*Sardinops sagax* *Vinciguerria* spp.

Assemblage	Summer	Autumn	Winter	Spring	Characteristic species (from SIMPER analysis)
Offshore assemblages					
Mixed Offshore	December 02_E December 03_D December 04_D December 04_E	April 03_D	August 02_D August 02_E August 03_C August 03_D	October 03_D October 03_E November 03_D November 03_E	*Lampanyctus* spp.
Summer Offshore	December 02_D February 03_C February 03_D February 03_E January 04_D January 04_E	April 03_E March 04_C April 04_D April 04_E	June 04_C		*Diaphus* "slender" spp *Vinciguerria* spp.
STSW			August 03_E	September 04_E	Not enough samples to calculate
Winter Offshore			July 04_B July 04_C July 04_D July 04_E August 04_C	September 04_C September 04_D	*Vinciguerria* spp *Lampanyctus* spp. *Cyclothone* spp.

Shelf assemblages were also largely distinguished by season, but with some exceptions. The *mixed shelf* assemblage, for example, contained samples from all seasons, and was characterised by moderate to high concentrations of the larvae of *S. sagax* (68%) (Table 2.6), with *Engraulis australis* (13%) and *Etrumeus teres* (5%) also abundant.

The *autumn mid-shelf* assemblage was also characterised by *S. sagax* (47%), as well as the more oceanic *Vinciguerria spp*. (40%), with Callionymidae sp. 1 larvae also common (13%). Larval fish concentrations within this assemblage were generally low. In contrast, the high diversity, very high concentration *summer shelf* assemblage was characterised by the presence of Labridae sp. 1 larvae (47%), with *S. sagax* (9%)

and *E. australis* (7%) also present. The *spring shelf* assemblage was also characterised by Labridae sp. 1 (37%), as well as *S. sagax* (13%), but these larvae were found at much lower concentrations than in the *summer shelf* assemblage.

Offshore assemblages contained larvae from oceanic families, such as the Myctophidae and Phosichthydae, and assemblages were largely distinguished by variations in the dominance of a few common taxa. The most characteristic taxon in the *mixed offshore* assemblage was *Lampanyctus* spp. larvae (15%) (Table 2.6), with larvae of *D. atlanticus* (23%), and *Vinciguerria* spp. (15%) also abundant. The *summer offshore* assemblage was characterised by *Diaphus* "slender" spp. (60%), and *Vinciguerria* spp. (10%), and was the highest concentration, highest diversity offshore assemblage. It was distinct from the *winter offshore* assemblage, which was characterised by *Vinciguerria* spp. (22%), *Lampanyctus* spp. (16%) and *Cyclothone* spp. (5%). The *winter offshore* assemblage also contained fewer *Diaphus* "slender" spp. larvae than the summer offshore assemblage. The *mixed offshore* assemblage contained less *Diaphus* "slender" spp. larvae than the *summer offshore* assemblage, and less *Hygophum* spp, and *Vinciguerria* spp. larvae than the *winter offshore* assemblage.

2.3.4 Interannual variability in larval fish assemblages

The degree of interannual variability present between the two and a half years sampled depended on the season, and station location sampled. Station A mostly contained the same assemblage at the same time of year throughout the study period (Table 2.6). However, November and March station A assemblages varied between years, and in June 2004, station A contained an *autumn mid-shelf* assemblage. Shelf

station (stations B and C) assemblages were more variable between years, with August station C, for example, having a different assemblage on each of the three occasions it was sampled. Station B in November, and station C in December had the same assemblage for two of the three years sampled, whereas the assemblages found during March at station B were the same in both years sampled. Stations B and C were sampled in August, November and December, during 2002, 2003 and 2004 (Table 2.6). Neither of the shelf stations sampled during these months supported the same assemblage for all three years. Some offshore stations (D and E) had the same assemblage during the two years sampled, such as station D during August 2002 and August 2003, and station E during April 2003 and April 2004. However, most offshore stations had different assemblages between years.

2.4 Discussion

2.4.1 Larval fish assemblage composition

Total larval fish concentrations off south-western Australia were comparable with those found off Eastern Australia (Smith and Suthers, 1999), in the Agulhas Current off South Africa (Beckley and Ballegooyen, 1992), in the Western Irish Sea (Dickey-Collas *et al*., 1996), and in the English Channel (Grioche *et al*., 1999). They were slightly higher than those found off the northwest shelf of Western Australia (Sampey *et al*., 2004: less than 1 larval fish per m^3), but lower than larval fish concentrations found off the more productive coasts of south-western Africa (Olivar and Shelton, 1993), and Peru (Vélez *et al.,* 2005: up to 14 larval fish per m^3). Larval fish concentrations in this study were also lower than those found in the California Current in 1975 (Loeb *et al*., 1983), and around the Canary Islands (Rodriguez *et al.,* 2004). It should be noted, however, that larval fish concentrations are dependent on net mesh

size and larval fish size, thus comparisons with concentrations from other studies of slightly different design will not be perfect.

The composition of the larval fish assemblages largely reflected the spawning locations of adult fish species. Inshore assemblages were dominated by the larvae of small inshore reef fishes, especially from families within the Blennioidei and Gobioidei, such as Tripterygiidae, Clinidae and Gobiidae, as well as species from within the Monacanthidae. Species within these families tend to have demersal eggs (Leis and Carson-Ewart, 2000), or in the case of Clinidae species, are live-bearers (Goodwin *et al*., 2002). These life-history characteristics can limit the offshore dispersal of eggs and larvae, and can result in increased persistence of these fish larvae in inshore environments (Suthers and Frank, 1991). Inshore larval fish assemblages were highly seasonal, with greater larval fish concentrations and species diversity in summer. Larvae from the Clinidae and Tripterygiidae were often the only species still found in autumn and winter inshore assemblages. Little is known about the spawning time periods of these families, but it appears that in this region, they spawn most of the year round.

Larval fish assemblages on the shelf contained the larvae of reef fish (e.g., Labridae, Monacanthidae), pelagic species, especially those from the Clupeiformes (*Sardinops sagax, Etrumeus teres*), and some oceanic larvae such as *Vinciguerria* spp., at particular times of year. Assemblage structure was shown to largely reflect the water mass present at the station sampled, with a species of labrid (Labridae sp. 1) strongly characteristic of summer shelf samples within the Capes Current water mass. There are about fifteen temperate species of labrid found off south-western Australia

(Hutchins and Swainston, 1986), but their spawning times are not well known. Most of the species which have been studied, such as *Choerodon* spp. (Fairclough, 2005) and *Bodianus frenchii* (Cossington, 2006) spawn predominantly in spring-summer.

Although abundances of *S. sagax* larvae were shown to distinguish between larval fish assemblages, concentrations of this species were not predictable with season, and *S. sagax* larvae were found in most shelf samples (see Chapter 4). This reflected the tendency for *S. sagax* to spawn through much of the year (Fletcher and Tregonning, 1992; Gaughan *et al*., submitted). The peak spawning season of *S. sagax* has been shown to be variable between different parts of Australia, with peak spawning occurring in June to October in sub-tropical southern Queensland, and in southern Australia in summer and autumn (Ward *et al.,* 2003). Spawning of this species may be linked to sea surface temperatures (SSTs), with Ward *et al*. (2003) suggesting that SSTs of 21° to 23°C are the most suitable for *S. sagax* spawning. However, in this study, samples containing high abundances of *S. sagax* larvae were found all year around, from locations where the SST ranged from 18.5° (August 2002), to 22.2° (April 2003), which reflected the findings of other Western Australian studies (e.g., Gaughan *et al.*, 1990; Kendrick, 1993).

Offshore larval fish assemblages were dominated by the larvae of oceanic families, such as the Myctophidae, Phosichthydae and Gonostomatidae. Patterns of reproduction among these families are generally not well known, but they often have protracted spawning seasons, or year-round spawning. Gartner (1993) found that there were generally two main reproductive patterns among Myctophidae species in the eastern Gulf of Mexico: either a protracted spawning season of 4-6 months duration,

such as with *Benthosema suborbitale* and *Lampanyctus alatus*, or more restricted spawning periods occurring once or twice a year, such as with *Ceratoscopelus* spp. and *Diaphus dumerillii*. In this study, offshore larval fish assemblages were largely distinguished by the relative abundances of *Diaphus* "slender" spp., *Vinciguerria* spp., and *Hygophum* spp. Most species of *Diaphus* for which data exist have been found to spawn during summer, with spawning season length varying among species and latitudes (Olivar, 1987; Moku *et al*., 2003; Sassa and Kawaguchi, 2004). In contrast, *Vinciguerria* spp. tend to spawn most of the year round (Richards, 2006b), while little is known about spawning habits of *Hygophum* spp. Seasonal differences in the abundances of larvae of these taxa are therefore likely to have been due to both seasonal differences in spawning of taxa such as *Diaphus* "slender" spp., as well as seasonal variations in advective transport of larval fish between summer and winter, related to the strength and position of the Leeuwin Current.

2.4.2 Larval fish assemblages and water masses

Larval fish assemblages and distributions may be strongly influenced by water mass structure and movement (Olivar and Beckley, 1994; Hare *et al*., 2001, 2002; Hsieh *et al*., 2005). In this study, water masses were found to be generally good predictors of larval fish assemblages, with assemblages within different water masses statistically different from each other. This was a result of changes in water mass structure being related to water depth and distance from the coast, with inshore species found in inshore water masses, and shelf and offshore species found in the Leeuwin Current, for example. Additionally, the presence of seasonal features, such as the Capes Current, were associated with distinctive assemblages containing high abundances of certain species, such as Labridae sp. 1. The oceanography of the region sampled was

highly seasonal, with a characteristic water mass structure present at different times of year (Pearce *et al*., in press). Adult fish spawning locations and seasonality, and seasonal changes in water mass movement therefore combined to result in the spatial and temporal structure of larval fish assemblages found.

It was not possible to examine interannual variability in larval fish assemblages in detail, due to the short duration of the study. However, it was noted that the interannual differences in assemblages observed between years were largely due to changes in the position of water masses. The study transect was sampled three times during the month of December during the two and a half years of sampling. In 2002, the larval fish assemblage at station C was classified as being a *spring shelf* assemblage, while in 2003 and 2004, a *summer shelf* assemblage was found at this station. Much higher larval fish concentrations were also present in 2003 and 2004, compared to 2002. Analysis of water mass structure at the times of sampling showed that in 2002, station C was located in the Leeuwin Current, while in 2003 and 2004, it was located in the Capes Current. These two currents flow in opposite directions, and have differing physical and biological properties (Gersbach *et al*., 1999; Hanson *et al.,* 2005), which resulted in the distinct larval fish assemblages found between them.

The timing of the change in the meteorological seasons also influenced the oceanographic structure of the region, and subsequently on the larval fish assemblages. In March 2003, the weather patterns preceding the cruise were characteristic of a summer regime, while in March 2004, they were more characteristic of winter (see Chapter 3). Consequently, the larval fish assemblage at

station A was a *summer inshore* assemblage in 2003, and a *winter inshore* assemblage in 2004.

Only two samples were taken beyond the seaward boundary of the Leeuwin Current during the study period. These samples were both from station E, in August 2003 and September 2004. On both occasions, station E was located very close to the border between the Leeuwin Current and Sub-tropical Surface Water, but the assemblages found in these two samples were significantly different to those taken within the Leeuwin Current itself. This suggests that, even in offshore waters where larvae of oceanic species dominate, the Leeuwin Current supports a larval fish assemblage that is distinct from Sub-tropical Surface Water, reflecting its tropical origin.

2.4.3 Similar larval fish assemblages within different water masses

While water mass was by far the best indicator of the larval fish assemblage at a location along the study transect, it was not a perfect predictor. Water mass gave a good indication of the larval fish assemblage present at inshore stations, but it was not as reliable for shelf stations. The eleven samples in the *summer shelf* assemblage were all collected within the Capes Current water mass, however, the *mixed shelf* assemblage consisted of nine samples from the Leeuwin Current, and three from the Capes Current. Similarly, the *spring shelf* assemblage contained two Capes Current samples, and ten Leeuwin Current samples. This occurrence of the same larval fish assemblage in different water masses was most apparent in the spring and summer months, when both the Capes Current and Leeuwin Current were affecting the study area.

The Capes Current is a wind-driven upwelling current, which tends to occur in "pulses" associated with periods of strong southerly wind stress (Gersbach *et al.,* 1999; Pearce and Pattiaratchi, 1999). These periods are related to the summer meteorological patterns over the south-west of Australia, in particular, the passage of high pressure cells over the region, and the formation of heat troughs over the west coast, which influences the strength of the coastal seabreeze (Yimin *et al.,* 2001). When southerly wind stress is weak, and air temperatures warm, due to the predominantly easterly winds, oceanographic conditions on the shelf are warm and stratified. There is generally a deep chlorophyll maximum layer present, and very low nutrients and phytoplankton biomass within the euphotic zone (Hanson *et al.,* 2005; Koslow *et al.*, 2005). After several days of strong southerly winds, the water column becomes unstratified, and cooler at the surface, and the Capes Current may flow more strongly northwards past the study area, bring cooler, higher salinity water from the south (Pearce *et al*., in press). Periods of strong southerly winds may also induce deep water from slope and offshore areas to upwell onto the outer shelf (Pearce *et al*., in press). The biological effects of these events are not well known, but it is probable that the high variability in spring and summer larval fish assemblages on the shelf was related to the timing of sampling with respect to these events, as well as the water mass present at the sampling stations. Samples ascribed to the *summer shelf* assemblage, for example, may therefore be representative of both a water mass type, and an oceanographic and meteorological situation at the time of sampling. Some species may be more sensitive to these variations in conditions than others, with larvae from the Clupeiformes showing particularly variable abundances (see Chapter 4).

Larval fish assemblages from autumn and winter samples had a higher affinity with the water mass present than those from spring and summer. Most samples from autumn and winter were either in winter inshore water, Leeuwin Current water, or Sub-tropical Surface Water, with larval fish assemblages corresponding accordingly. Spatial connectivity across the shelf appeared to be greater in autumn and winter, with samples from stations B, C, D and E mostly in the same water mass (the Leeuwin Current), and samples from the outer three stations on the same cruise frequently containing the same larval fish assemblage. This connectivity was not as evident during summer, apart from in the upper surface layer, due to periodic offshore Ekman transport (see Chapter 5).

2.4.4 Variation of larval fish assemblages within water masses

A number of larval fish assemblages were associated with the Leeuwin Current, but samples from the same station and season within the current did not always contain the same assemblage. Samples from shelf stations inundated by the Leeuwin Current were distinct from those taken in offshore waters of the Leeuwin Current, suggesting that water depth had a structuring effect on assemblages not completely related to water mass position. This was probably due to the differing spawning locations of adult fish of different species such as *S. sagax*, which usually spawn on the shelf (Fletcher, 1990), and oceanic Myctophid species, which spawn in deeper water (Sassa *et al*., 2004a). There was also some seasonality within offshore Leeuwin Current assemblages. Of the three offshore larval fish assemblages found in association with the Leeuwin Current, the *summer offshore* assemblage was found in summer and autumn, mostly when sea surface temperatures were >21°C, and the *winter offshore* assemblage was found in winter and spring, mostly when sea surface temperatures

were <20°C. The *summer offshore* assemblage was also associated with low concentrations of larvae of tropical species during summer and autumn, which represented another potential source of seasonality in Leeuwin Current assemblages. The *mixed offshore* assemblage was found all year around, with sea surface temperatures at the time of sampling ranging between 18 - 22.5°C.

Larval fish assemblages collected from within the Capes Current were also variable. Most Capes Current samples contained a *summer shelf* assemblage, however, three Capes Current samples contained a *mixed shelf* assemblage, two November samples contained a *spring shelf* assemblage, and two March samples contained a *March inner shelf* assemblage. Variability in Capes Current larval fish assemblages was therefore largely temporal, with spring and autumn assemblages different from summer ones. The three Capes Current samples containing a *mixed shelf* assemblage were distinguished from the *summer shelf* assemblages by their lower concentrations of Labridae sp. 1 larvae. No obvious reasons were found for this result.

2.5 Conclusions

Overall, the initial hypothesis that the structure of larval fish assemblages would reflect regional oceanographic processes was largely confirmed. Assemblages were strongly aligned to water masses, with assemblages between water masses significantly different from each other. Distance from shore and water depth were also important, sometimes independent of water mass, suggesting an influence of the spawning locations of adult fish of different species on larval fish assemblage structure. However, results from this study suggest that, while broad distinctions may be made between assemblages from different water masses, meteorological and

oceanographic conditions (some on relatively short time-scales), may be influential in further structuring larval fish assemblages.

Chapter 3: Correlation of environmental and meteorological variables with larval fish assemblages off south-western Australia

3.1 Introduction

Larval fish distributions are initially determined by adult spawning locations, and modes of egg development (Leis and Carson-Ewart, 2000; Cowen, 2002). Once larvae have hatched, their temporal and spatial positions are further influenced by both their abiotic and biotic environments, and their behaviour in response to their environment. Larval fish densities are also influenced by survival rates, as a result of starvation from lack of food, and predation mortality (Lasker, 1975; Bailey and Houde, 1989). As a result, the formation and maintenance of larval fish assemblages is largely dependent on both spatial and temporal variability in oceanographic and biological conditions, the favourability of conditions for larval fish survival, and the behavioural responses of larvae of different species to these conditions.

Larval fish assemblages are often seasonal, as a result of seasonal changes in oceanographic and biological conditions (Gray, 1993; Espinosa-Fuentes and Flores-Coto, 2004). Adult fish may also spawn at specific times to allow their larvae to hatch into advantageous conditions for feeding, or retention (Bakun, 1985; Sinclair, 1988; Cushing, 1990). Distinctive larval fish assemblages tend to be associated with different water depths, as a result of both adult fish spawning locations, and differences in water mass structure and properties with distance offshore (Gray, 1993; Cowen *et al.*, 1993; Franco-Gordo *et al*., 2001; Hare *et al*., 2001).

Larval fish assemblages within a particular region would therefore be expected to

have a broad scale temporal and spatial structure (see Chapter 2). However, smaller-scale meteorological and oceanographic events may also be influential. Storm events may result in greatly increased turbulence and mixing, and increased Ekman transport (Maillet and Checkley, 1991), with different larval fish assemblages persisting before and after such events (McKinnon *et al*., 2003). Stratification within the water column, and the depth of sampling relative to the base of the mixed layer may also influence the larval fish assemblage found (Smith *et al.*, 1999; Marancik *et al*., 2005). The distribution and abundance of potential prey items within the water column also affects larval fish feeding, growth and survival, and thus the larval fish assemblage (Munk *et al*., 2004; Sanchez-Velasco *et al*., 2004b). These biological characteristics are in turn heavily influenced by oceanographic and meteorological events, such as upwelling, and periods of strong winds (Lasker, 1975; Simpson, 1987). The meteorological, oceanographic and biological parameters that influence larval fish assemblages are therefore linked, both in time and space.

Biophysical and oceanographic conditions off south-western Australia are unique, largely as a result of the characteristics of the dominant regional-scale current: the Leeuwin Current. Unlike other eastern boundary currents, the Leeuwin Current is a poleward flowing, downwelling current, which results in low nutrient and productivity levels and warm water off the south-western Australian coast (see Chapters 1 and 2). In contrast to many other coastal oceans, chlorophyll α biomass in these waters peaks in winter (Lourey *et al*., 2006). The correlation of larval fish assemblage structure to environmental variables in this area is therefore of interest, as it may help to understand how planktonic organisms, such as fish larvae, respond to their oligotrophic, oceanographically unique environment off Western Australia. The

elucidation of which environmental factors are most closely correlated to larval fish assemblages can assist in understanding factors that structure assemblages in time and space, and those that may regulate survival and recruitment.

This study aimed to correlate larval fish assemblages to a range of environmental variables, including meteorological, physical and biological parameters. It was hypothesised that the strongest correlations to larval fish assemblages would be with those variables showing strong seasonal patterns, reflecting the strong seasonal structure found within larval fish assemblages (see Chapter 2). However, meteorological and biological events on shorter time-scales than seasons were also expected to show some influence.

3.2 Materials and Methods

3.2.1 Environmental variables

Larval fish assemblage data were collected for two and a half years, along a five station transect off south-western Australia (see Chapter 2 for full sampling details). Assemblage data were correlated with 13 environmental variables (Table 3.1), using BVSTEP (a procedure based on BIOENV) in Primer-6 (see below). The environmental variables chosen for analyses represented physical, chemical, biological and meteorological variables. All variables were chosen as measurable variables, which may reasonably be expected to correlate with larval fish assemblages and which were collected simultaneously during the SRFME sampling program (see Appendix 2 for all environmental data).

Meteorological data were collected at Rottnest Island by the Western Australian

Bureau of Meteorology. Rottnest Island was considered the best meteorological sampling station to use to approximate conditions in coastal and shelf waters (see Figure 1.1 for location of Rottnest Island).

Table 3.1: Environmental variables correlated with larval fish assemblages collected on the Two Rocks transect, August 2002 to December 2004. Meteorological variables represent a mean value for the five days prior to sampling. CM denotes chlorophyll maximum layer, which was variable, and determined from prior CTD sampling.

Meteorological variables	**Physical and chemical variables**	**Biological variables**
Maximum air temperature (°C)	Fremantle Mean Sea Level (cm) (monthly mean)	Maximum chlorophyll α (mg chlα/m^3)
Solar radiation (MJ/m^2)	Fremantle Mean Sea Level anomaly from 14yr mean (cm)	Chlorophyll α at surface (mg/m^3)
Wind speed (m/s)	Sea surface temperature (°C) (SST)	Microzooplankton (no./L) at surface
Wind direction (from) (°) (standardised from 270°)	Salinity at surface	Microzooplankton (no./L) at CM
	Nitrates and nitrites (NO_x) (μmoles/L) at surface	

Meteorological variables were averaged for the five days prior to sampling. This timescale was selected to incorporate the lag between meteorological conditions, and larval fish responses to subsequent biological processes (Checkley *et al*., 1988; Maillet and Checkley, 1991; Baumann *et al.*, in press). The microzooplankton data had some data points missing for some cruises (all stations in October and November 2003, stations C in December 2002, and station D in April 2004). As the BVSTEP procedure cannot be run with missing values, these sample dates were removed from the analyses. Environmental variable values were individually transformed prior to

analysis, and then normalised, to remove the effects of different scales of measurement. The appropriate transformation was determined by examination of the skewness of each variable, using draftsman plots, also in Primer-6 (Clarke and Warwick, 2001). For BVSTEP and PCA analyses only, wind direction data were converted from a circular measure (0-360°) into a linear measure. Perusal of the raw wind data revealed few data points around 270° (i.e., westerly), therefore, wind data were standardised by calculation of the distance of each bearing from 270°. Bearings of <270° were converted by subtraction from 270, while bearings of >270° were converted by subtracting them from 360, and then adding 270.

Physical variables were sourced from CTD casts taken concurrently with larval fish samples, from the SRFME Biophysical Oceanography project (see Chapter 2) (Koslow *et al.*, 2005). Fremantle mean sea level (FMSL) data were provided by the National Tidal Centre (P. Davill), and represented a proxy for the strength of the Leeuwin Current (Pearce and Phillips 1988; Feng *et al.* 2004). FMSL anomaly refers to the difference between the recorded sea level, and the long term (14 year) mean for each month (Pearce *et al.,* unpublished data).

Chlorophyll α biomass data were calculated using JGOFS protocols (Koslow *et al.*, 2005), and were used courtesy of S. Pesant *et al.* (unpublished data), and the SRFME Biophysical Oceanography project. Microzooplankton cell concentrations included every heterotrophic/mixotrophic organism between 20 – 200 µm, and all protists >200 µm. Common taxa included species from the Stobilididae, Strombidiidae, Tintinnina and dinoflagellates. These data were collected from 850mL seawater samples, fixed in 10% acid Lugols, which were taken at the surface and at the chlorophyll maximum

layer (CM). Data were provided courtesy of Paterson (2006).

Spatial and temporal variability within the environmental parameters measured was explored by plotting them against the day of the year at which they were taken, for each sampled station. Meteorological data were not plotted separately for each sampled station, as all data were sourced from one meteorological sampling station only (Rottnest Island). Third-order polynomial lines of best fit were shown for each variable, with R^2 values, to aid interpretation.

Two-way analysis of variance (ANOVA) in SPSS for Windows 14.0 was used to test for the presence of significant differences between nitrate/nitrite concentrations, chlorophyll concentrations and microzooplankton concentrations between sampling stations, and between seasons, with Tukey's post-hoc test used for pairwise comparisons. The presence of an interaction effect between water depth and season was also tested for. T-tests were used to compare concentrations of environmental variables between the surface and CM.

3.2.2 Multivariate analyses

The structuring effects of all environmental variables on all stations where larval fish were collected were examined using PCA. This technique used Euclidean distance similarities to plot points (representing sampled stations) in two-dimensional space as an ordination. The distance between points represented their similarity to each other, in terms of the environmental variables included in the analysis. Stations were plotted along principal components, or axes, in a way that best described the variation in the data: i.e., the dimensionality of the dataset was reduced in such a way that the

maximum amount of information was retained (Clarke and Warwick, 2001). The principal components were therefore linear combinations of the original variables, and were not correlated to each other.

The BVSTEP sub-routine in Primer-6 was used to determine which subset of the full suite of environmental variables provided the best match with complementary larval fish assemblage data, and whether that match was statistically significant (at $p<0.05$) (Clarke and Warwick, 2005). The reference matrix used in this routine was a triangular similarity matrix constructed from assemblage data, using Bray-Curtis similarities. The second matrix contained the environmental variable data (for variables shown in Table 3.1). During the BVSTEP procedure, subsets of environmental variables were drawn from the full suite, and used to construct Euclidean distance matrices, which were then correlated with the reference similarity matrix using the Spearman rank correlation coefficient (ρ: maximum of 1) (Clarke and Ainsworth 1993). The results indicated the proportion of variance in the assemblage data explained by the environmental variables (Clarke and Ainsworth 1993; Kelmo *et al.,* 2003). Fish larvae concentration data were transformed as described in Chapter 2.

BVSTEP analyses were carried out on the whole two and a half year data set, and then on various sub-groups of the data. Samples were first grouped by station (A – E), and analysed separately. For this analysis, stations D and E were combined, due to lower sample numbers, and the similarity in the water mass found at these two stations throughout the study period (i.e., the Leeuwin Current). Assemblage sub-groups from each season (summer, autumn, winter, spring) were also separated and analysed.

Where a statistically significant ($p<0.05$) result was returned, the combination of variables that were best correlated to the larval fish assemblages was noted (to a maximum of six variables).

3.3 Results

3.3.1 Spatial and temporal patterns within environmental variables

Meteorological variables

Most of the meteorological variables measured showed a seasonal pattern, although this was more pronounced for some variables. Both maximum air temperature and solar radiation had minimum values during winter, and maximum values during summer (Figure 3.1). Wind speed and wind direction (0-360°) showed a less clear seasonal pattern. Wind speed was variable throughout the year, but was generally lowest during autumn, and most variable during winter (Figure 3.1). Wind direction was on average more southerly during summer (around 150 to 180°), and tended more south-westerly during winter (around 200 to 250°).

Physicochemical variables

Sea surface temperature and salinity were strongly seasonal at station A (Figure 3.2). Both variables were at a minimum during late winter, and a maximum during late summer. Water temperature at the surface at station B was also strongly seasonal, with minimum values in late winter, and maximum values in late summer. Salinity at station B was also seasonal, however, changes in salinity through the year were not as pronounced as at station A (about 0.6 variability, compared to about 1.0). Salinity at station B was highest in summer, and lowest in winter, however some variability, especially in autumn and spring, was evident.

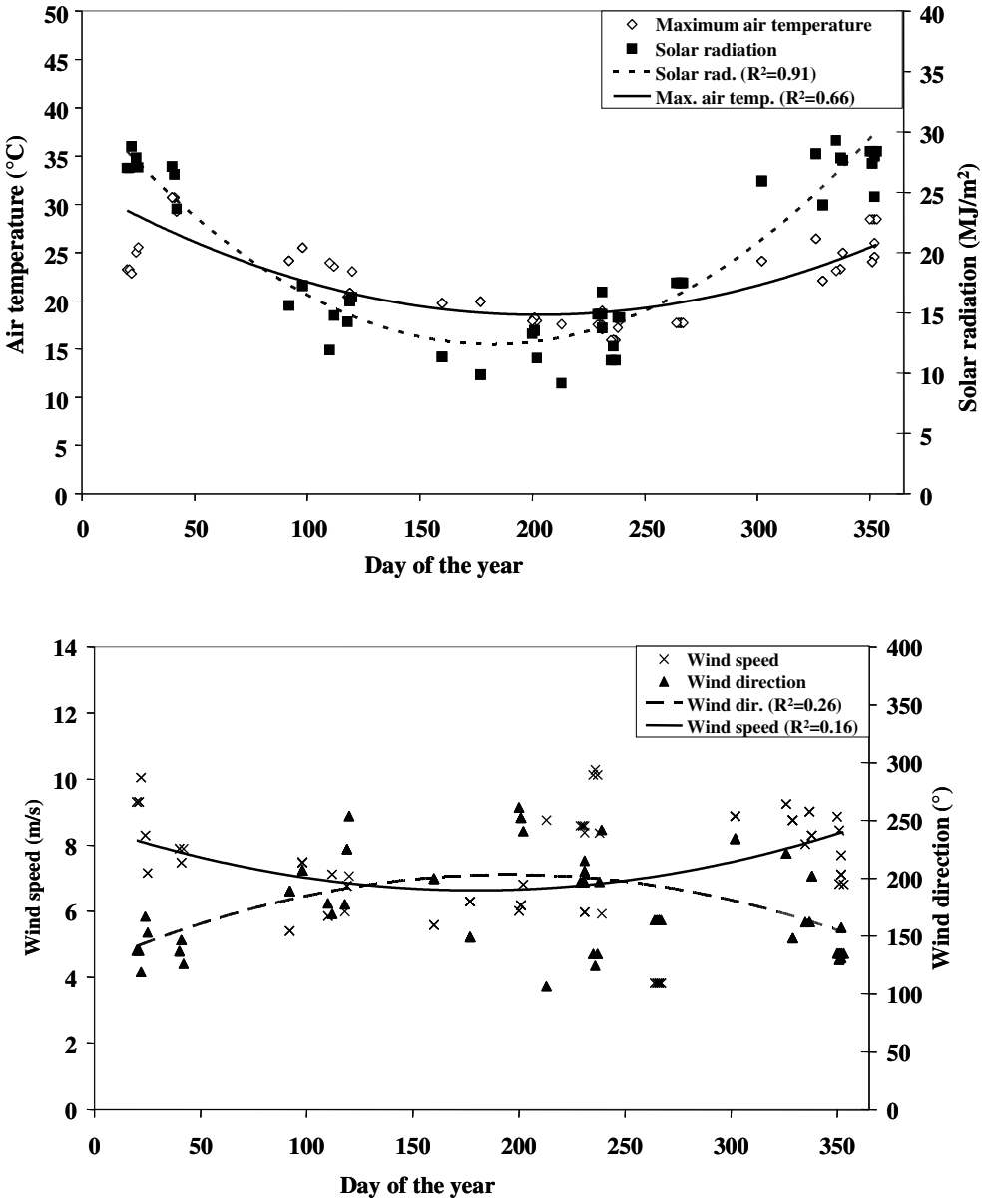

Figure 3.1: Variation in four meteorological variables through the year, showing mean values for the five days prior to larval fish sampling (August 2002 to December 2004). Third-order polynomial curves are fitted to the data, with R^2 correlations shown. All meteorological data were collected at Rottnest Island.

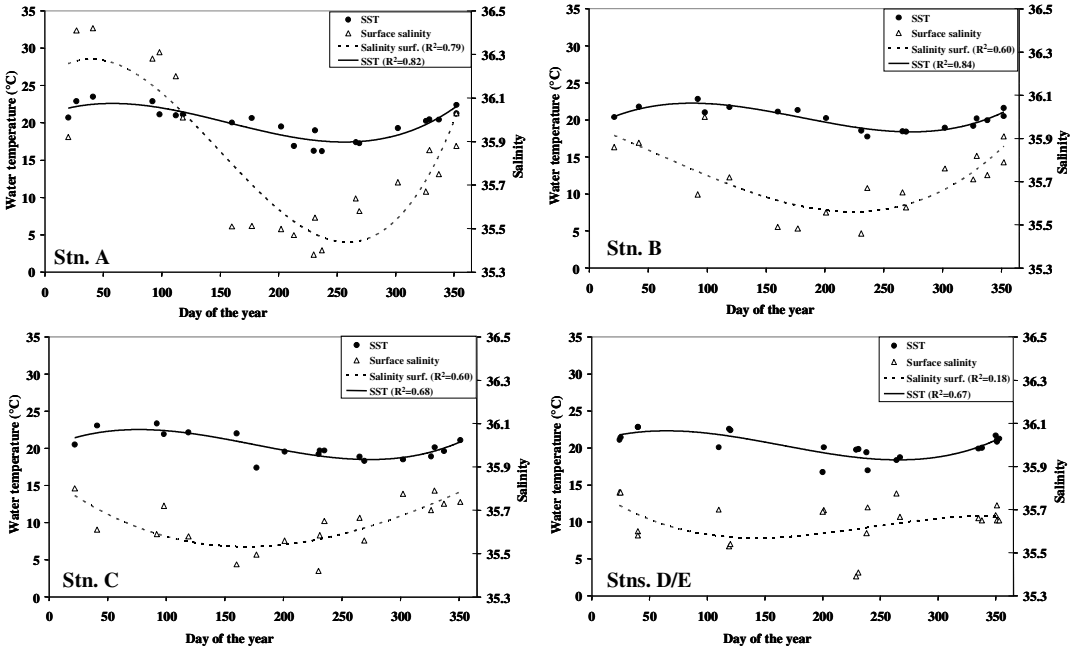

Figure 3.2: Variation in sea surface temperature and salinity through the year from CTD casts taken during larval fish sampling on the Two Rocks transect (August 2002 to December 2004). Data are shown for stations A, B, C and D/E separately. Third-order polynomial curves are fitted to the data, with R^2 correlations shown.

Sea surface temperature at station C was also seasonal, although with less change through the year than at station A (Figure 3.2). Salinity showed a weak seasonal trend, but was variable. Temperature and salinity at stations D and E were the least seasonal out of all stations sampled. Some samples from winter showed low salinity, however values for both parameters did not vary widely throughout the year (Figure 3.2).

Fremantle mean sea level (FMSL) is a proxy for Leeuwin Current strength (Pearce and Phillips 1988; Feng *et al.* 2004), and varied with a seasonal pattern (Figure 3.3). Lowest values were recorded in spring, and highest values in autumn. FMSL and

surface salinity were compared using linear regression, for station C data. A significant, negative linear correlation was found (R^2=0.40, p=0.003) (Figure 3.3B). The FMSL anomaly was calculated by comparing the monthly FMSL for the Two Rocks sampling period to a long-term (14 year) monthly mean (Figure 3.3C). The FMSL anomaly for the study period was generally negative, especially in spring and summer, indicative of a weaker than average Leeuwin Current over the study period.

Nitrate and nitrite (NO_x) concentrations were higher in autumn and winter than in summer (p<0.001, p=0.001) or spring (p<0.001, p=0.003) (Figure 3.4). NO_x concentrations were also higher at stations A than at any other of the sampled stations (p<0.001 for all). Concentrations at station B were generally low, with no pronounced seasonal signal. One unusually high value was recorded in April 2003 (autumn) (Figure 3.4). NO_x concentrations at stations C, D and E were also generally low, and not strongly seasonal, however, some higher values were recorded in autumn and winter. There was a significant interaction between water depth and season in this analysis, suggesting that the influence of water depth was dependant on season, and vice versa.

Biological variables

Chlorophyll α biomass concentrations through the water column were highly variable (Figure 3.5). Concentrations were significantly higher at the CM than at the surface (p=0.04). Surface concentrations were higher in autumn and winter than in summer (p=0.03, p<0.001), and higher in winter than in spring (p=0.03).

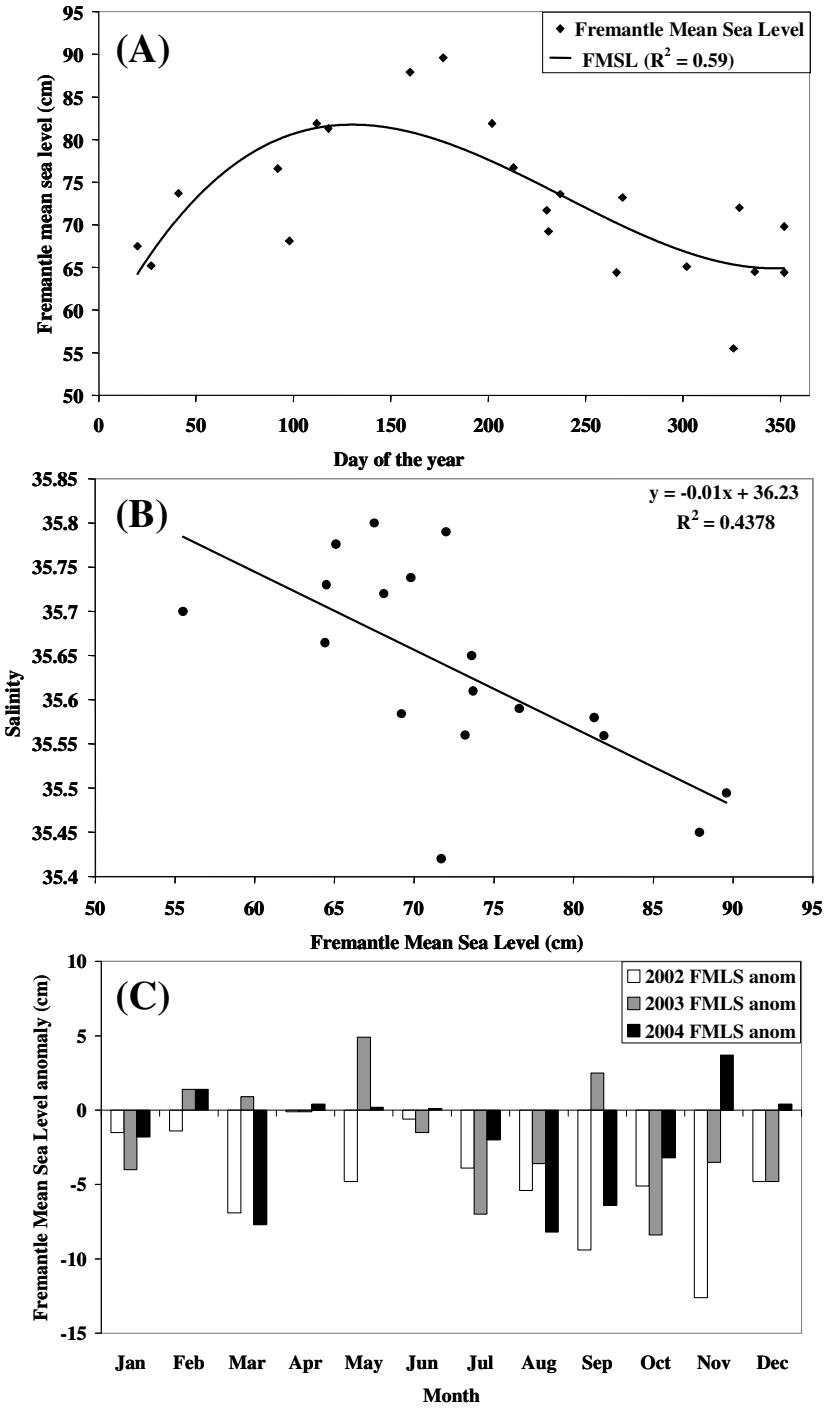

Figure 3.3: Monthly mean of Fremantle mean sea level (FMSL): (A) FMSL through the year with third-order polynomial curve fitted, (B) Linear correlation of FMSL with surface salinity at station C (100m depth), (C) FMSL anomaly: deviation from the 14 year monthly mean. Data courtesy P. Davill (National Tidal Centre) and A. Pearce (CSIRO Marine and Atmospheric Research).

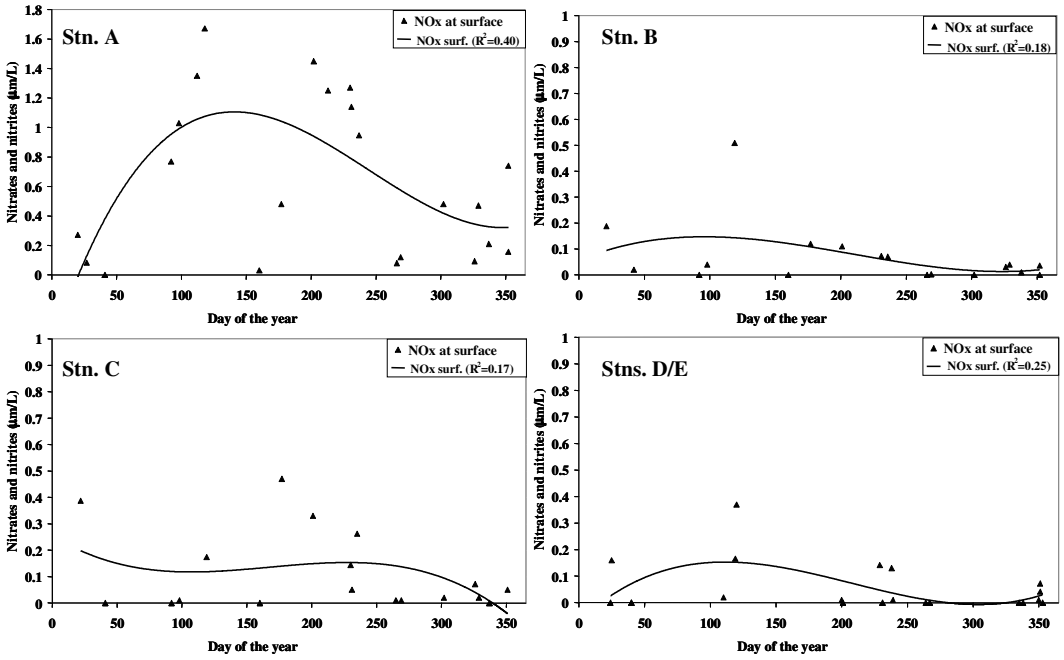

Figure 3.4: Variation in nitrates and nitrites (NOx) concentration, at the surface through the year, collected simultaneously with larval fish data from the Two Rocks transect (August 2002 to December 2004). Data are shown for stations A, B, C and D/E separately. Third-order polynomial curves are fitted. Note different scale at station A.

Unlike NO_x and microzooplankton concentrations, surface chlorophyll α biomass did not vary markedly between stations (no statistically distinct comparisons at $p<0.05$). There was no interaction between water depth and season in this case ($p=0.13$). Maximum chlorophyll α biomass was less seasonal, with a significant decrease between autumn and spring ($p=0.01$) the only significant result.

Microzooplankton concentrations were significantly higher at the surface than at the CM ($p=0.02$). Surface microzooplankton concentrations were also higher at station A than at station E (Figure 3.6), and also higher in winter than in summer ($p=0.001$), or spring ($p<0.001$).

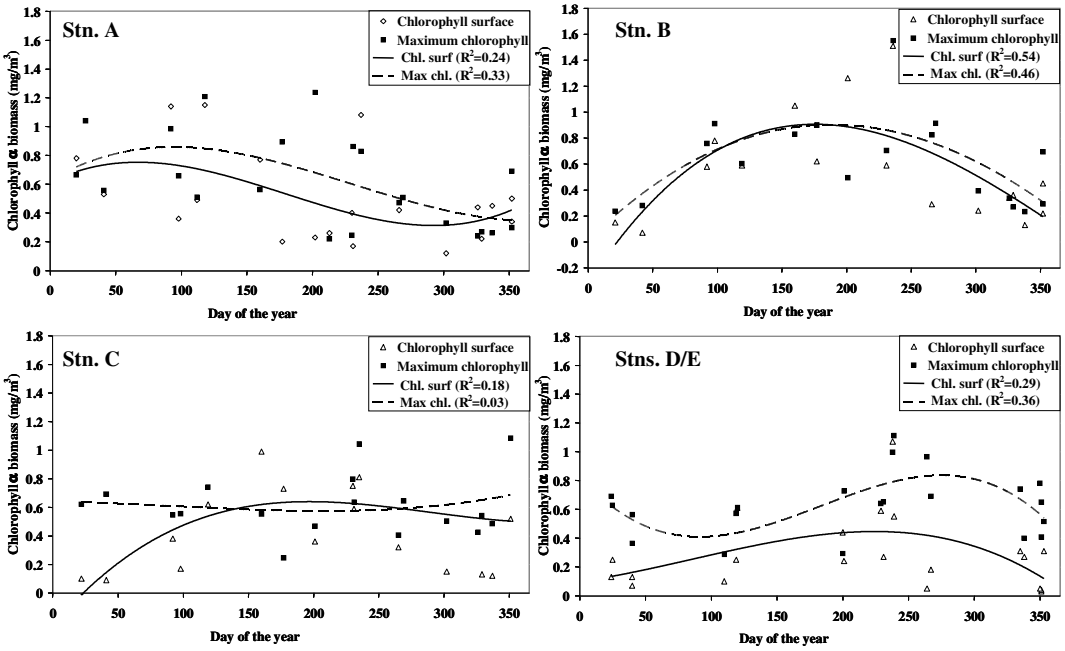

Figure 3.5: Variation in chlorophyll α biomass, at the surface and chlorophyll maximum layer through the year, collected from samples taken simultaneously with larval fish assemblage samples from the Two Rocks transect (August 2002 to December 2004). Data are shown for stations A, B, C and D/E separately. Third-order polynomial curves are fitted.

At the CM, there was no significant difference between microzooplankton concentrations between different stations. However, concentrations were higher in summer than in autumn (p=0.02), or spring (p=0.002). There were no significant interactions between water depth and season in either of these analyses. Patterns of abundance at the surface were often different from those at the CM, especially at stations A and B, with concentrations at the CM often less variable (Figure 3.6).

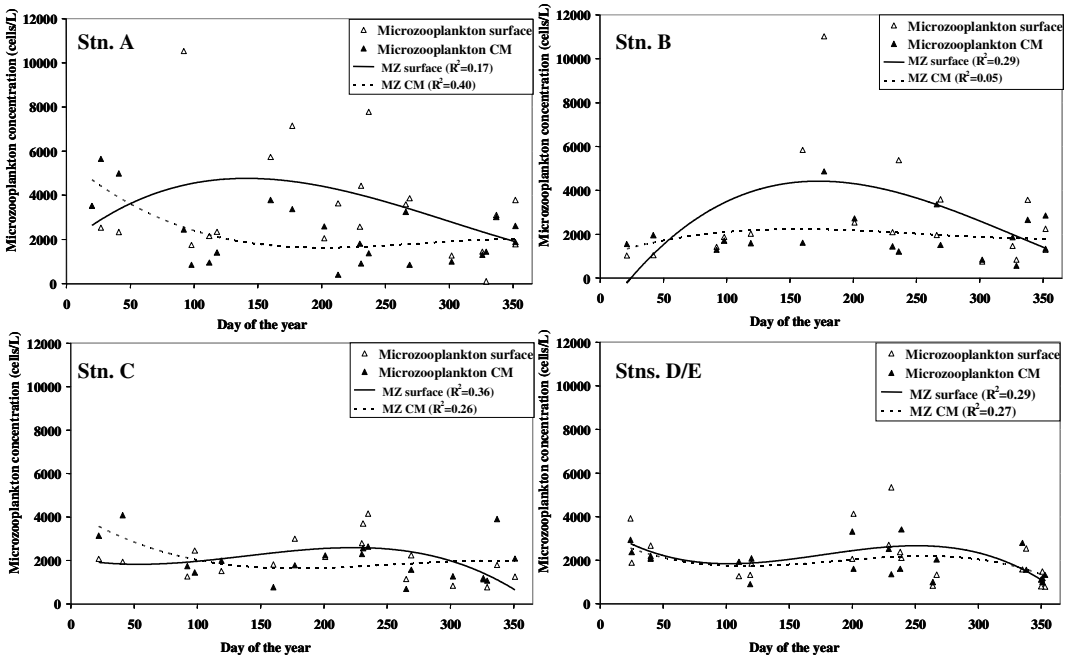

Figure 3.6: Variation in microzooplankton concentrations, at the surface and chlorophyll maximum layer (CM) through the year, collected simultaneously with larval fish data from the Two Rocks transect (August 2002 to December 2004). Data are shown for stations A, B, C and D/E separately, courtesy Paterson (2006). Third-order polynomial curves are fitted.

Mesozooplankton data are not yet available for the whole study period. However, mesozooplankton concentrations analysed from February 2002 to February 2003 indicated a peak in abundance in autumn at stations A, B and C, and minimum concentrations in winter and spring (J. Strzelecki, unpublished data). In summer and autumn, mesozooplankton concentrations at station A were higher than at shelf and offshore stations, while in winter and spring, concentrations were similar between sampled stations across the transect.

3.3.2 PCA analyses

Principal components analysis of all sampled stations using all thirteen environmental variables resulted in the generation of five principal component axes (PCs) (Table 3.2). Between all five PCs, 74% of the variation among stations was explained.

Table 3.2: Eigenvalues for five principal components constructed from PCA analysis of all sampled stations, August 2002 to December 2004. Cumulative percentage of variation in stations explained by each PC is also shown.

PC	%Variation explained	Cumulative % Variation explained
1	28	28
2	17	45
3	11	56
4	10	66
5	8	74

Eigenvectors for principal component 1 (PC1) and principal component 2 (PC2) only were examined for each environmental variable, to determine which variables were most influential in structuring samples along these axes (Table 3.3).

PC1 was a seasonal axis. Samples with positive values along PC1 (positive eigenvectors), were associated with high concentrations of microzooplankton at the surface, high chlorophyll α biomass at the surface, and high FMSL (i.e., a strong Leeuwin Current), while samples with negative values along this axis were associated with high solar radiation, high maximum air temperatures, and high surface salinity.

Along PC2, samples were strongly structured by FMSL and FMSL anomaly, as well as sea surface temperature. Stations with negative eigenvectors along PC2 were associated with high FMSL, and high FMSL anomaly (i.e., a strong Leeuwin

Current), and high sea surface temperature, as shown by the strong negative eigenvectors associated with these variables (Table 3.4). In contrast, samples with positive values along PC2 were found at times of weak Leeuwin Current flow, and cooler water temperatures.

Table 3.3: Eigenvectors resulting from principal components analysis of all samples from August 2002 to December 2004. Eigenvectors are shown for each environmental variable, for each of five principal components. FMSL denotes Fremantle Mean Sea Level, a proxy for the strength of the Leeuwin Current, CM denotes chlorophyll maximum layer.

Environmental variable	Eigenvectors	
	PC1	PC2
FMSL	0.32	-0.43
FMSL anomaly	-0.05	-0.55
Sea surface temperature	-0.22	-0.48
Salinity surface	-0.24	-0.21
NO_x surface	0.20	-0.01
Maximum chlorophyll	0.24	-0.14
Chlorophyll surface	0.30	-0.04
Microzooplankton surface	0.32	-0.16
Microzooplankton CM	0.04	-0.27
Maximum air temperature	-0.44	-0.22
Solar radiation	-0.48	0.07
Wind speed	-0.17	0.17
Wind direction	0.19	0.17

PCA ordination of all sampled stations using PC1 and PC2 showed strong separation between summer and winter stations along PC1 (Figure 3.7). Summer was therefore associated with high solar radiation, high maximum air temperatures, and high surface salinity, while winter stations were sampled at times of high FMSL, high concentrations of microzooplankton at the surface, and high chlorophyll α biomass at the surface. Autumn and spring stations were best separated along PC2, with the positive values for spring samples suggesting an association with a weak Leeuwin Current, and negative values for autumn samples reflecting maximum Leeuwin

Current flow during this season. PC1 and PC2 were therefore both seasonal axes, but showed maximum and minimum values at different seasons through the year.

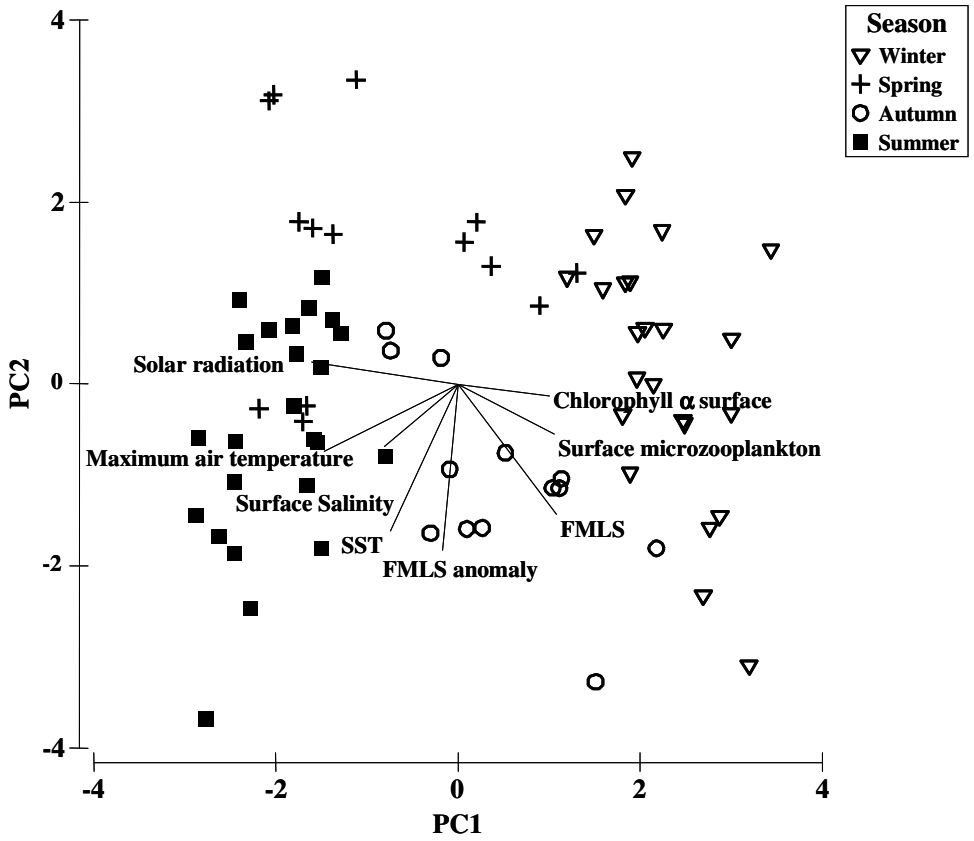

Figure 3.7: PCA ordination of all sampled stations by PC1 and PC2, August 2002 to December 2004, using thirteen environmental variables. Stations are coded by season. Vectors are shown for the eight most influential environmental variables, along PC1 and PC2.

3.3.3 BVSTEP analyses

Larval fish assemblages were correlated with all available environmental variables using the BVSTEP sub-routine. When all assemblages from all sampled stations were analysed, a combination of wind speed, sea surface temperature, surface salinity and NO_x at the surface returned the highest correlation (ρ=0.31, p=0.001) (Table 3.4). Assemblages from station A only were significantly correlated to maximum air temperature and FMSL (ρ=0.56, p=0.001). Assemblages from station B were

correlated with a combination of solar radiation, FMSL and microzooplankton concentrations at the CM (ρ=0.58, p=0.003).

Table 3.4: Results of BVSTEP analyses between all environmental variables, and sub-sets of the larval fish assemblage data. The result of analysis of all samples is shown, as well as results of analyses including samples from each sampling station (A to E) separately. Samples were taken along the Two Rocks transect, August 2002 to December 2004, off south-western Australia. FMSL denotes Fremantle Mean Sea Level, CM denotes the chlorophyll maximum layer. * denotes result significant at p<0.05, ** denotes result significant at p<0.01.

BVSTEP test between:	**Combination of variables giving best correlation. Spearman coefficient (ρ) and significance level (p) are shown**
All samples	Wind speed Sea surface temperature Surface salinity NO_x at the surface (ρ=0.31, p=0.001**)
Station A samples	Maximum air temperature FMSL (ρ=0.56, p=0.001**)
Station B samples	Solar radiation FMSL Microzooplankton at the CM (ρ=0.58, p=0.003**)
Station C samples	Solar radiation Wind speed Sea surface temperature Microzooplankton at the surface (ρ=0.40, p=0.03*)
Stations D and E samples	Sea surface temperature Surface salinity NO_x surface Maximum chlorophyll α biomass Microzooplankton at the surface and CM (ρ=0.47, p=0.004**)

Larval fish assemblages from station C were best correlated with four environmental variables: solar radiation, wind speed, sea surface temperature and microzooplankton at the surface (ρ=0.40, p=0.03). Assemblages from stations D and E were significantly correlated with a combination of sea surface temperature, surface salinity, NO_x at the surface, maximum chlorophyll a biomass, and microzooplankton at the surface and the CM (ρ=0.47, p=0.004) (Table 3.4).

When the BVSTEP procedure was repeated, this time within sub-groups of samples from each season, all four analyses (winter, spring, summer and autumn groupings) returned significant results (Table 3.5). Winter larval fish assemblages were best correlated with five environmental variables: FMSL anomaly, sea surface temperature, surface salinity, NO_x at the surface and microzooplankton at the surface (ρ=0.58, p=0.001). Spring assemblages were best correlated to wind speed, NO_x at the surface and maximum chlorophyll α biomass (ρ=0.57, p=0.019). Summer larval fish assemblages were best correlated to surface salinity only (ρ=0.42, p=0.002). Autumn larval fish assemblages were best correlated to wind direction, sea surface temperature, surface salinity, NO_x at the surface and chlorophyll α biomass at the surface (ρ=0.58) (Table 3.5).

Table 3.5: Results of BVSTEP analyses between all environmental variables, and seasonal sub-sets of the larval fish assemblage data collected on the Two Rocks transect, August 2002 to December 2004. SST denotes sea surface temperature, FMSL denotes Fremantle Mean Sea Level. * denotes result significant at p<0.05, ** denotes result significant at p<0.01.

BVSTEP test between:	**Combination of factors giving best correlation. Spearman coefficient (ρ) and significance level (p) are shown**
Winter samples	FMSL anomaly SST Surface salinity NO_x at the surface Microzooplankton at the surface (ρ=0.58, p=0.001**)
Spring samples	Wind speed NO_x at the surface Maximum chlorophyll α biomass (ρ=0.57, p=0.02*)
Summer samples	Surface salinity (ρ=0.42, p=0.002**)
Autumn samples	Wind direction SST Surface salinity NO_x at surface Chlorophyll α biomass at the surface (ρ=0.62, p=0.002**)

3.4 Discussion

3.4.1 Seasonal and spatial variability in environmental conditions across the Two Rocks transect

Physical, biological and meteorological variables examined during this study showed predominantly seasonal trends. Summer was characterised by high air temperatures and high solar radiation, and high surface salinity at inshore and shelf stations. Winter was characterised by high FMSL (i.e., a strong Leeuwin Current), and relatively high concentrations of NO_x, chlorophyll α biomass, and microzooplankton concentrations

at the surface, especially inshore. Autumn was associated with highest FMSL (i.e., strongest Leeuwin Current flow), high sea surface temperatures and high NO_x concentrations, while spring was characterised by lowest FMSL (i.e., weakest Leeuwin Current flow), low sea surface temperature and low microzooplankton concentrations. As PCA analyses showed, both meteorological and oceanographic seasonal patterns in the physical and biological environmental were evident, operating at slightly different time-scales. Meteorological variables, such as air temperature, followed meteorological seasons, with minimum values in winter, and maximum values in summer. In contrast, oceanographic variables such as FMSL (i.e., the strength of the Leeuwin Current) were at a minimum in spring, and a maximum in autumn. This result highlights the lag between changes in the meteorological seasons, and influences on the Leeuwin Current, via seasonality in current strength through the Indonesian Throughflow (Godfrey and Golding, 1981).

An increase in nutrients and chlorophyll biomass in late autumn, through winter to early spring was evident across the sampled transect. This pattern has been documented recently off south-western Australia (Hanson *et al*., 2005; Lourey *et al*., 2006; Fearns *et al*., submitted), and contrasts with the seasonal cycle of productivity in other eastern boundary currents. In the Benguela Current, for example, chlorophyll concentrations are at a maximum from spring to autumn (Andrews and Hutchings, 1980; Brown and Field, 1986; Koné *et al*., 2005), while in the Humboldt Current, along the Peruvian coast, maximum chlorophyll concentrations occur in both late spring and autumn (Echevin *et al*., 2004). These chlorophyll maxima off both southern Africa and South America are associated with upwelling strength, and are found within seasons characterised by upwelling-favourable wind conditions.

Upwelling off the south-western Australian coast is negligible, and primary productivity cycles are driven by other mechanisms. These may include the deepening of the mixed layer in late autumn and winter, and subsequent nutrient entrainment into the euphotic zone (Lourey *et al*., 2006). However, the autumn and winter maximum in nutrients and chlorophyll α biomass did not coincide with maximum larval fish concentrations (see Chapter 2).

3.4.2 Correlation of larval fish assemblages to environmental variables: temporal patterns between seasons

While many of the environmental variables analysed in this study showed strong seasonal cycles, most did not reveal strong spatial patterns. It should be noted, however, that meteorological data were only collected at one station (Rottnest Island), while other variables were measured at each station separately. Meteorological variables used in these analyses therefore had no spatial component. Some biological parameters, such as NO_x and microzooplankton concentrations, tended to be higher at inshore stations, but in general, seasonal patterns were dominant. However, analyses of larval fish assemblages collected across the Two Rocks transect suggested that assemblages were initially defined by sampling station, with the strength of this pattern changing seasonally (see Chapter 2). This association was largely a result of both the spawning locations of adult fish, and water mass structure and movement; a result found in other parts of the world (e.g., Cowen *et al*., 1993; Gray, 1993; Smith *et al*., 1999; Hare *et al*., 2001). However, the source and nature of temporal changes in larval fish assemblages were less clear. Correlation of larval fish assemblages with meteorological, physicochemical and biological data of a more continuous, rather than categorical, nature was designed to investigate this.

Larval fish assemblages at station A were strongly seasonal, and were closely associated with two seasonal variables: maximum air temperature and FMSL. However, as mentioned, these variables had different seasonal patterns. Larval fish assemblages at station A were therefore correlated to both meteorological and oceanographic seasons. The physical dynamics of the inshore lagoon off Two Rocks, where station A was situated, underwent large temperature and salinity changes between seasons, as a result of changes in air temperatures and evaporation rates. Water movement in this area was also highly seasonal, with strong southward flow in winter, and generally northward flow in summer (Gersbach *et al*., 1999; Fandry, *et al.,* 2006). However, current reversals in coastal waters on short-time scales may occur in response to the wind climate, especially in summer (Masselink and Pattiaratchi, 1998). Nutrient concentrations at station A changed seasonally, with NO_x levels inshore increasing abruptly in autumn, and decreasing again in spring (Koslow *et al*., 2005). This was probably due to increased mixing, and nutrient resuspension as a result of winter storm events (Maillet and Checkley, 1991; Gallucci and Netto, 2004), and terrestrial and groundwater sources, due to increased rainfall (Lourey *et al*., 2006). Strong seasonal distinctions in coastal larval fish assemblages therefore reflected strong seasonality in their environment.

Environmental conditions, and larval fish assemblages, at station B were also largely seasonal. Spring and summer larval fish assemblages were associated with higher solar radiation, and lower FMSL (i.e., weaker Leeuwin Current) than autumn and winter assemblages. The inclusion of microzooplankton at the CM as a structuring environmental variable suggests that common processes may have been influencing

both larval fish assemblages and microzooplankton concentrations, however, high microzooplankton concentrations were usually present when there were low larval fish concentrations. Microzooplankton concentrations, at the surface in particular, were highest in winter and spring, and lowest in summer and autumn. This was in contrast to larval fish concentrations at station B, which were highest in spring/summer, and lowest in winter (see Chapter 2). Zooplankton abundance and composition has been found to impact on larval fish assemblages, or may vary in a similar way to larval fish, in response to environmental features (Munk *et al*., 2004; Hsieh *et al.,* 2005), but in this case, the response of microzooplankton and larval fishes to environmental variables was evidently different. It should be noted, however, that the microzooplankton data used here were standing stock only, and did not take production into account.

Limited data on mesozooplankton were available, however, it appeared that spatial and temporal variability in mesozooplankton concentrations were not particularly well aligned to variability in either larval fish concentrations or microzooplankton. Mesozooplankton concentrations appeared to peak in autumn, especially inshore, with minimum concentrations in winter and spring (J. Strzelecki, unpublished data). Microzooplankton concentrations were highest in winter, and larval fish concentrations were highest in spring and summer. Planktonic organisms feeding at different trophic levels, and completing their life cycles at different temporal and spatial scales, could therefore have different responses to their physical environment across the sampled transect.

Larval fish assemblages at station C also showed some seasonal structure, and were

correlated to solar radiation, sea surface temperature and wind speed. This correlation may reflect both a seasonal structure to assemblages, and an influence of recent wind events. During the austral autumn, the meteorological regime changes from a southerly wind-dominated summer situation to a winter situation, typified by lower mean wind speeds, with occasional very strong north-westerly to south-westerly winds as a result of the passage of cold fronts (Masselink and Pattiaratchi, 2001; Yimin *et al.*, 2001). Storm events, and to a lesser extent, strong southerly seabreezes in summer, may break down stratification within the water column, and lead to an increase in nutrient concentrations in the mixed layer, and subsequent phytoplankton blooms (Checkley *et al.*, 1988; Maillet and Checkley, 1991). Larval fish distribution and survival have been linked to both the concentration and distribution of patches of primary and secondary productivity within the water column (e.g., Lasker, 1975; Maillet and Checkley, 1991). Some distinction may therefore exist between larval fish assemblages associated with a mixed water column, found after periods of high wind speed, and a stratified water column. The passage of storm fronts over the study area during autumn and winter may have influenced larval fish assemblages on the shelf, within the broader-scale seasonal structure.

At stations D and E, both physicochemical and biological variables were correlated to larval fish assemblages. At these stations, sea surface temperature was at a maximum, and surface salinity at a minimum, during autumn, when the Leeuwin Current was flowing at its strongest. This season was also associated with highest NO_x concentrations in offshore waters, and minimum microzooplankton concentrations. Larval fish assemblages at stations D and E were therefore seasonal, and correlated to seasonal changes in physical, chemical and biological variables.

Larval fish assemblages across the sampled transect showed strong seasonal structure. However, assemblages were also correlated to some parameters which may vary on a shorter timescale than seasons. BVSTEP analyses suggested that larval fish assemblages from particular stations and seasons were significantly correlated to wind speed, microzooplankton concentrations and NO_x at the surface. These variables may change significantly on time-scales of days to weeks (Johannessen *et al.*, 1995; Porter *et al*., 2005), and may have influenced larval fish assemblages on relatively short time scales. However, as the timing of our sampling was carried out on a broader time-scale than these meteorological and biological cycles, their effects were not as clearly visible as they may have been, had samples been taken at shorter time intervals.

3.5 Conclusions

The environmental variables analysed in this study showed strong seasonal patterns, which were reflected in the strong seasonal variability in larval fish assemblages. In contrast, environmental variables generally showed weak spatial structure. Inshore larval fish assemblages were the most seasonally predictable, and best separated by environmental variables, with offshore assemblages the least so. Meteorological and biological influences on larval fish assemblage structure at shorter time-scales than seasons, such as storms, and associated physicochemical and biological responses to these events, were noted. Sampling on a shorter time-scale than in the SRFME program would be required to quantify the effects of these events on larval fish assemblages.

Chapter 4: Influence of reproductive cycles and environmental variables on temporal and spatial patterns of clupeiform larvae off south-western Australia

4.1 Introduction

Small pelagic clupeiform fishes such as sardine (*Sardinops sagax*) and anchovies (*Engraulis* spp.) are ubiquitous in cool to warm temperate coastal oceans worldwide, and are particularly abundant in eastern boundary current systems (Parrish *et al*., 1989; Olivar *et al*., 2001; Smith *et al.,* 2001). They are an important component of many marine food webs, and may support substantial fisheries (Beckley and van der Lingen, 1999; FAO, 2004). For example, the total combined annual catch of all herrings, sardines and anchovies between 1994 and 2003 ranged from 4.1 million to 15.0 million tonnes off South America, and between 1.6 million and 2.3 million tonnes off southern Africa (FAO, 2004). However, recruitment to populations of these species is often highly variable from year to year, resulting in large fluctuations in stock sizes, and catches (Beckley and van der Lingen, 1999; Schwartzlose *et al*., 1999; Smith and Moser, 2003).

Much of the variability in adult population sizes, and spawning biomass of these species has been linked to climatic and environmental variables (Beckley and van der Lingen, 1999 and references therein). The stock size of the sardine in the California Current region was shown to undergo a precipitous decline in the 1940s and 1950s, followed by a rapid recovery in the 1980s. These patterns were not entirely related to fishing pressure: a major environmental change in the northeast Pacific occurred in the 1970s, with a shift from a “cool-ocean” to a “warm-ocean” oceanographic pattern

(Smith and Moser, 2003). This regime shift resulted in marked changes in abundance of a number of fish species, including the sardine and anchovy. In the Benguela Current ecosystem off southern Africa, recruitment of both sardine and anchovy has been linked to variability in sea surface temperature (which approximates upwelling events), and larval fish retention indices, as well as fishing pressure in more recent decades (Cole, 1999).

The El Niño phenomenon has also been implicated in changes in sardine and anchovy stock sizes. The El Niño event of 1997-98 led to reduced abundance of the sardine in the Gulf of California (Avalos-Garcia *et al*., 2003; Sanchez-Velasco *et al*., 2004a) and off Mexico (Funes-Rodriguez *et al*., 2001). However, sardine and anchovy populations do not tend to respond to environmental variation in the same way, and may vary out of phase, with decreased abundance of one species often accompanied by increased abundance of the other (Lluch-Belda *et al*., 1989; Baumgartner *et al*., 1992; Beckley and van der Lingen, 1999; Cubillos and Arcos, 2002).

The variability in recruitment to adult populations of both sardine and anchovy has been partially linked to varying rates of survival in early life history stages (Logerwell and Smith, 2001; Coombs *et al*., 2003, Smith and Moser, 2003). Different environmental conditions result in different retention, transport and feeding conditions for pelagic fish larvae, with subsequent impacts on recruitment (Lasker and Smith, 1976: Painting *et al*., 1998; Smith and Moser, 2003). The nature and extent of these impacts, and the discrepancies between the response of sardine and anchovy populations to the same climatic forcing may be predicted by consideration of the biology of the two species.

The sardine is generally found in association with upwelling areas, with the highest catches recorded off California, Peru and southern Africa (Beckley and van der Lingen, 1999). They typically spawn in continental shelf waters, and display a protracted spawning season (Beckley and van der Lingen, 1999, Olivar *et al*., 2003; Smith and Moser, 2003). The timing of spawning may differ between geographical regions (Ward *et al*., 2003). Environmental conditions have been shown to influence the time and place of sardine spawning, with maximum spawning activity occurring at times, and in locations, where deleterious offshore transport is at a minimum, and larval fish food concentrations are favourable (Le Clus, 1990; Gaughan *et al*., 2004; Santos *et al*., 2004; Somarakis *et al*., 2006). Concentrations of sardine eggs and larvae at the same place and time of year may therefore show considerable interannual variability (Fletcher *et al*., 1994; Gaughan *et al*., 2001b; Smith and Moser, 2003).

In regions where the two species co-occur, anchovy generally spawn closer inshore than sardines (Beckley and Hewitson, 1994; Smith and Moser, 2003; Curtis, 2004). Peak spawning of anchovy is often at times of year when sea surface temperatures are highest, and when the water column is stratified (Olivar *et al*., 2001; Ward *et al*., 2003; Avalos-Garcia *et al*., 2003). Feeding conditions have been shown to be optimal for anchovy larvae within a stratified water column (Lasker, 1975; Bergeron, 2000), while sardine may spawn into conditions characterised by higher mixing rates, and higher overall productivity (Palomera and Olivar, 1996; Lloret *et al*., 2004). Anchovy larvae usually show a shallower vertical distribution in the water column than sardine larvae, especially at night (Fletcher, 1999; Nakata *et al*., 2000; Olivar *et al*., 2001). These differences in the biology and behaviour of sardine and anchovy result in

potentially different responses of these species to environmental conditions, and to broader-scale climatic processes.

While both sardine and anchovy are found in the eastern Indian Ocean, off the coast of Western Australian, stock sizes and catches of both species are insignificant by world standards. The annual sardine catch, for example, has yet to reach 20 000t (Lenanton *et al*., 1991; Gaughan *et al*., 2001b). This is largely due to the lower productivity of south-western Australian coastal waters: a product of the downwelling, poleward-flowing Leeuwin Current (see Chapter 1). Pelagic larval fishes which feed in south-west Australian neritic waters would therefore be expected to grow at slower rates than those in higher productivity systems in other eastern boundary currents (Gaughan *et al*., 2001a), with implications for larval fish starvation, and mortality by predation (Bailey and Houde, 1989). However, the relationships between larval sardine and anchovy, and their physical and biological environment, have not been well studied off Western Australia, with the exception of some work completed along the south coast, east of Albany (approximately 34-35°S, and 118-122°E) (Fletcher and Tregonning, 1992; Gaughan *et al*., 2001a, 2001b).

This study aimed to document the temporal and spatial variability in abundance of larval sardine (*Sardinops sagax*) and anchovy (*Engraulis australis*) and of other clupeiform larvae, along a transect off the south-western coast of Australia, and relate this to known spawning seasons and environmental variables. It was hypothesised that larvae would be found at maximum abundance after periods of high spawning activity (as shown by GSI data), and when both feeding and retention conditions were favourable.

4.2 Materials and methods

4.2.1 Larval fish concentrations

Larval fishes were initially collected with bongo nets as described in Chapter 2, across a five station transect running from inshore (station A) to offshore (station E) waters. Clupeiform larvae were identified to species where possible using the descriptions in Neira *et al.* (1998). Concentrations (larvae/m^3) of all Clupeiform species found were calculated using flowmeter data, as described in Chapter 2. The lengths (mm SL) of all individuals of *Sardinops sagax*, *Engraulis australis* and *Etumeus teres* collected at each station on each cruise were measured using an eyepiece micrometer, to 0.1mm accuracy. Where more than 50 larvae of any species were collected in the one tow, a sub-sample of 50 randomly selected larvae was measured.

Larval concentrations of each species were compared to each other using linear regression in SPSS 14.0, to examine the possibility that concentrations of some species covaried. To show the direction of the observed correlations, b-coefficients were noted for each analysis where a significant result was returned. A b-coefficient value of >0 indicated a positive correlation, while values of <0 indicated a negative correlation.

4.2.2 Clupeiform species spawning seasons

The gonadosomatic index (GSI) of a fish is defined as the ratio of the weight of the ovaries to its body weight (GSI = (ovary weight/fish weight) x 100) (DeVlamming *et al*., 1982). It may be used to determine the spawning period of a species of fish, and

has been found to be an appropriate indicator of reproductive condition in other clupeids (Somarakis *et al*., 2004).

GSI data has not been extensively collected, or published, for clupeiform species found off Western Australia. Dimmlich *et al*. (2004) examined GSI of *Engraulis australis* caught off South Australia, but no similar study has been completed off Western Australia. Similarly, little GSI data has been collected for *Etrumeus teres*. However, some GSI data collected from adult female *Sardinops sagax* caught by the Fremantle fishery were available from the Department of Fisheries, Western Australia (DFWA), from 2000 to 2005 (Table 4.1). This included the period of larval fish sampling (August 2002 to December 2004). The Fremantle sardine fishery operates in nearshore and inner shelf waters off the Perth area, including grounds to the west of Carnac Island, and around Rottnest and Garden Islands (D. Gaughan, DFWA, *pers. comm*. 2006). As data were obtained opportunistically from the commercial fishery, some months had much more data than others. However, data were available for all months, except January, in at least one year over the period of larval fish sampling.

Linear regression was used to compare sardine GSI data for the period of larval fish sampling (August 2002 to December 2004), to larval sardine concentrations, to investigate whether higher adult spawning activity corresponded to higher larval fish concentrations.

Table 4.1: Availability of gonadosomatic index (GSI) data for adult *Sardinops sagax* caught off south-western Australia by the Fremantle fishery, 2000 to 2005. Number of observations (individual fish sampled) are shown. Data courtesy D. Gaughan and T. Leary, Department of Fisheries, Western Australia.

Month/Year	2000	2001	2002	2003	2004	2005
January	0	0	5	0	0	0
February	0	0	8	0	16	0
March	0	0	92	69	6	72
April	118	131	105	92	107	45
May	105	33	152	0	48	0
June	73	19	64	0	26	0
July	128	7	160	70	130	22
August	96	0	46	0	48	21
September	43	12	91	14	0	18
October	33	0	70	0	57	0
November	0	64	61	28	16	28
December	0	47	32	0	1	0

4.2.3 Relationships between larval fish concentrations and environmental variables

Relationships between clupeiform larvae concentrations and environmental variables were investigated using stepwise multiple linear regression. The environmental variables used in these analyses represent a subset of the variables used in PCA and BVSTEP analyses in Chapter 3. These variables represented those considered most likely to influence clupeiform larvae, given other reported correlations and trends in the published literature, and are shown in Table 4.2.

Table 4.2: Environmental variables used in multiple linear regression analyses to compare with larval concentrations of clupeiform fishes. CM denotes chlorophyll maximum layer. FMSL data provided by National Tidal Centre, courtesy P. Davill. Microzooplankton data courtesy Paterson (2006).

Physical and chemical variables	Biological and meteorological variables
Fremantle Mean Sea Level (cm)	Maximum chlorophyll α in water column (mg/m^3)
FMSL anomaly from 14 year mean (cm)	Chlorophyll α at the surface (mg/m^3)
Sea surface temperature (°C)	Microzooplankton cell concentrations (no./L) at surface
Surface salinity	Microzooplankton cell concentrations (no./L) at CM
Nitrates and nitrites (NO_X) at the surface ($\mu moles/m^3$)	Wind speed (m/s)
Day of the year	

Each environmental variable was examined, and then transformed if required, to remove skewness, and to approximate a normal distribution as much as possible (see Chapter 3). As a result, microzooplankton concentrations at the surface were $\log_{(x+1)}$ transformed, and maximum chlorophyll α was square-root transformed, prior to regression analyses. The environmental variables that combined to explain the maximum variance in larval concentrations of each species, at $p<0.05$, was noted for each of the most common three clupeiform species.

4.3 Results

4.3.1 Temporal and spatial patterns in clupeiform larval concentrations

Clupeiform fish larvae were found throughout the year across the sampled transect, with highest larval concentrations on the continental shelf (stations B and C) (Figure 4.1).

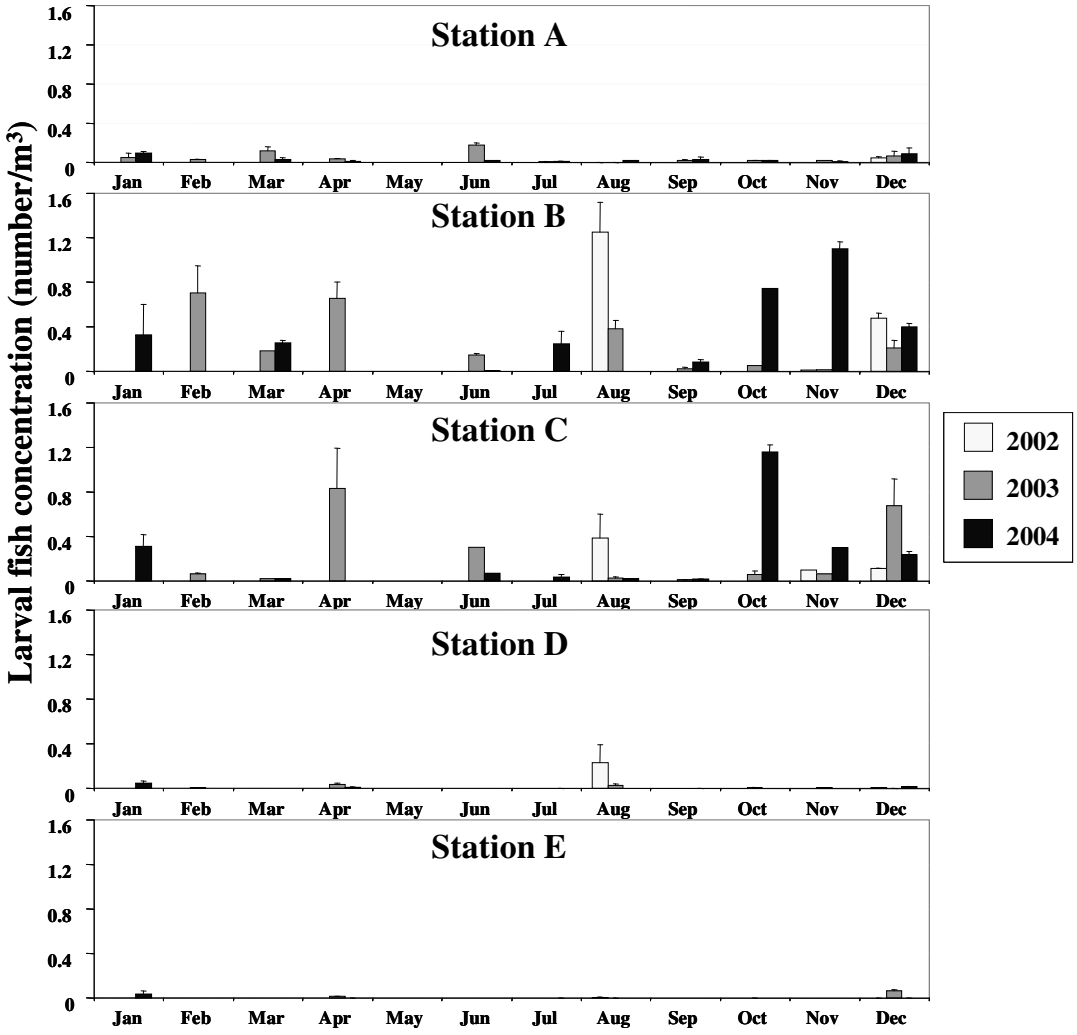

Figure 4.1: Concentration (number/m^3) of all clupeiform larvae at stations A to E on the Two Rocks transect, August 2002 to December 2004.

Concentrations on the shelf were often highly variable between years (e.g., see August and November). Four species of clupeiform were found: *Sardinops sagax*, *Etrumeus teres, Engraulis australis* and *Spratelloides robustus* (Appendix 3).

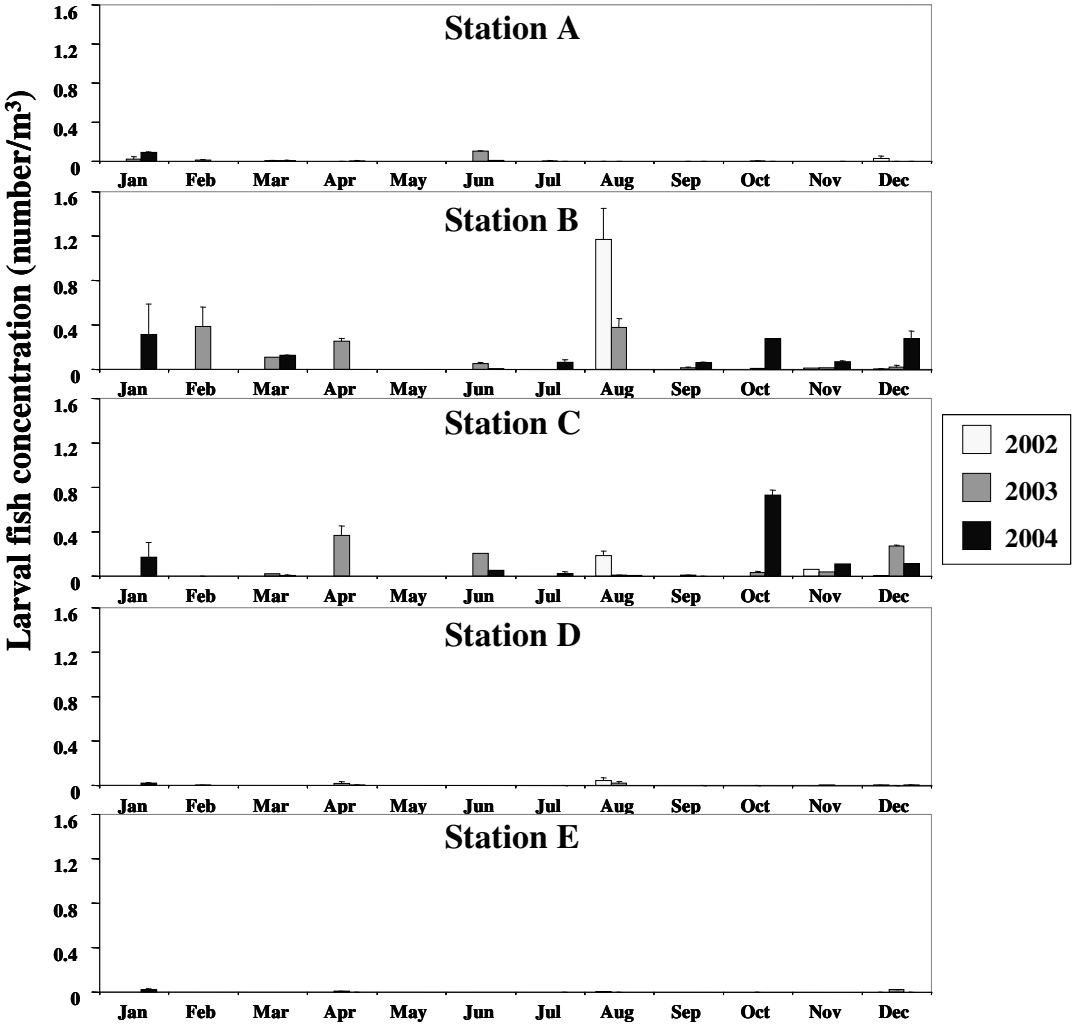

Figure 4.2: Concentration (number/m^3) of *Sardinops sagax* larvae at stations A to E on the Two Rocks transect, August 2002 to December 2004.

Sardinops sagax (sardine) was the most abundant species found across the Two Rocks transect, especially on the shelf, where it contributed 31% of the station B assemblage, and 22% of the station C assemblage (see Chapter 2). It was also found

in lower numbers at station A (2%), and station D (3%). Sardine larvae were present in samples collected throughout the year on the shelf, with a maximum mean concentration of 1.2 larvae/m^3 at station B in August 2002 (Figure 4.2).

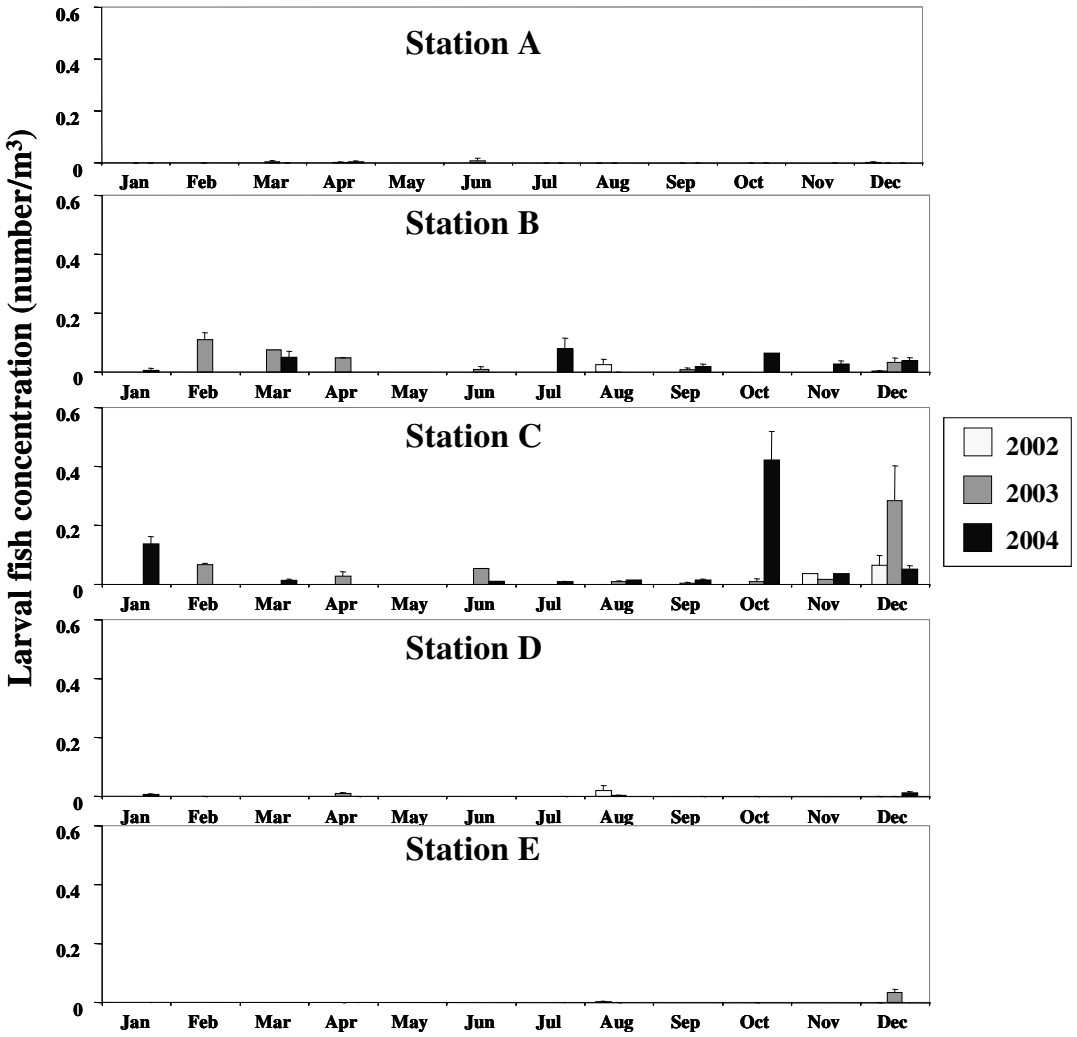

Figure 4.3: Concentration (number/m^3) of *Etrumeus teres* larvae at stations A to E on the Two Rocks transect, August 2002 to December 2004.

Engraulis australis larvae were found in inshore and shelf waters at most times of year, with peak abundance from spring to autumn (Figure 4.4). This species made up 3% of the station A assemblage, 13% of the station B assemblage and 2% of the

station C assemblage. Peak mean concentrations of this species were found in November 2004 at station B (1.0 larvae/m^3).

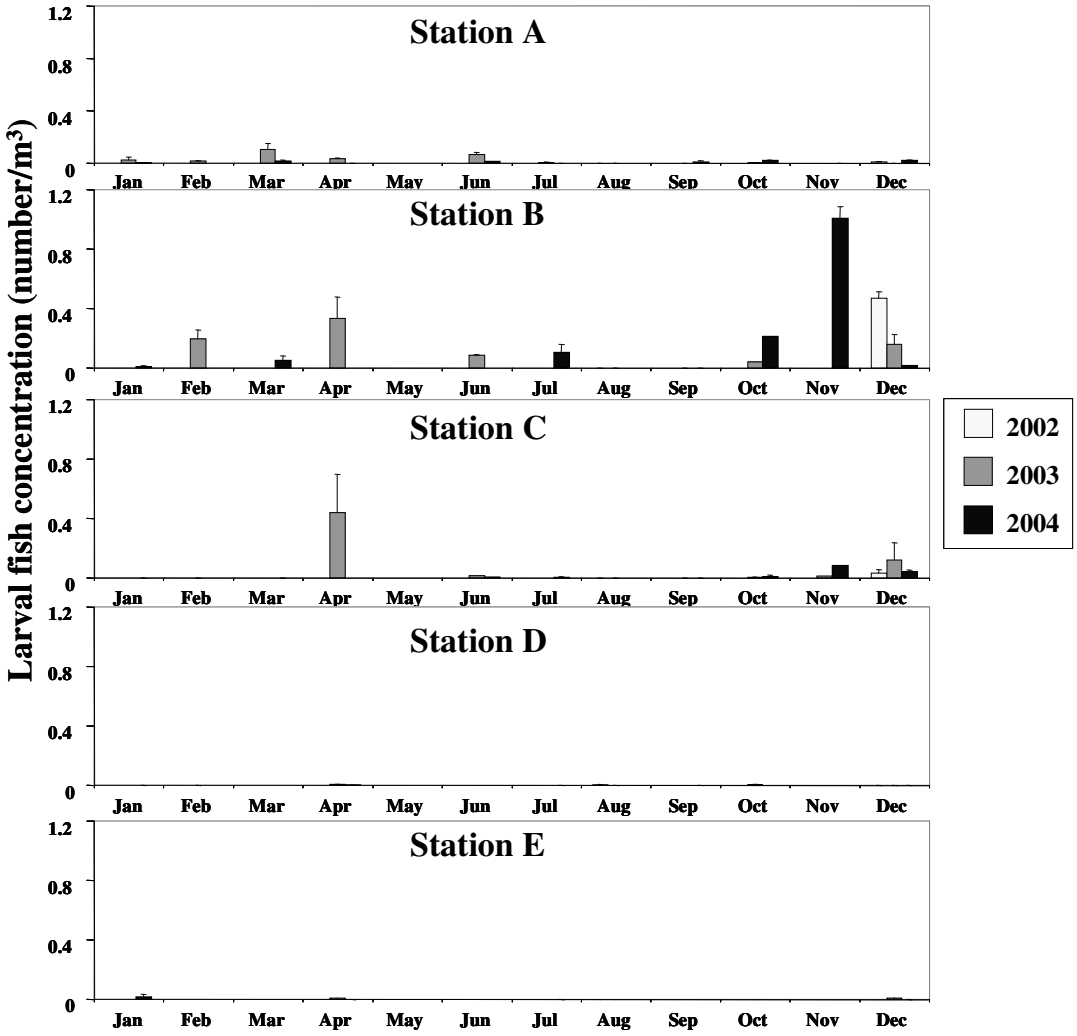

Figure 4.4: Concentration (number/m^3) of *Engraulis australis* larvae at stations A to E on the Two Rocks transect, August 2002 to December 2004.

Spratelloides robustus larvae were rarely found throughout the study, and only at stations A and B. Larvae of this species were most abundant at station A in early summer (Figure 4.5).

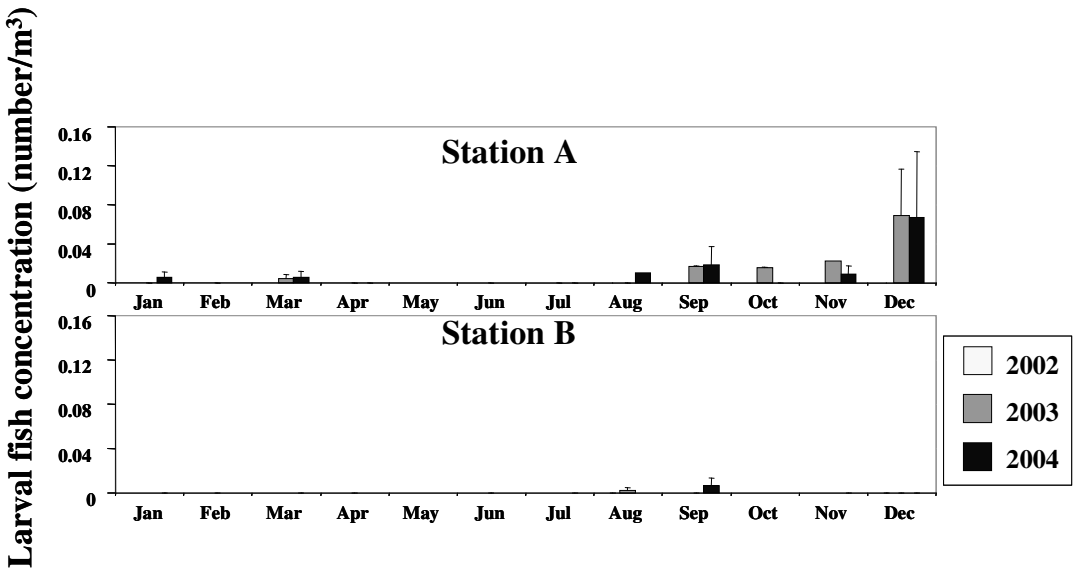

Figure 4.5: Concentration (number/m^3) of *Spratelloides robustus* larvae at stations A to B on the Two Rocks transect, August 2002 to December 2004.

4.3.2 Correlations between concentrations of larvae from different species and sampling stations

Linear regression between concentrations of the *S. sagax*, *E. teres* and *E. australis* for stations B and C showed the tendency of high concentrations of *S. sagax* and *E. teres* to be found at the same time at station C, with an R^2 statistic of 0.67 (Table 4.3). None of the other regression analyses completed returned a significant result. Larval fish concentrations were then compared between the inner shelf station (station B), and the outer shelf station (station C), for each species separately. Concentrations at the two stations were not correlated throughout the year for *S. sagax* (p=0.35), *E teres* (p=0.38), or *E. australis* (p=0.12).

Table 4.3: Results of linear regression analysis between concentrations of *Sardinops sagax, Etrumeus teres* and *Engraulis australis* collected on the Two Rocks transect at stations B (40m depth) and C (100m depth), August 2002 to December 2004. ** denotes result significant at p<0.01.

Species examined	Station	R-square (b-coefficients shown for significant results at p<0.05)	p
Sardinops sagax vs. *Etrumeus teres*	B	0.06	0.18
Sardinops sagax vs. *Etrumeus teres*	C	0.67 (b=1.2)	<0.001**
Sardinops sagax vs. *Engraulis australis*	B	-0.03	0.46
Sardinops sagax vs. *Engraulis australis*	C	0.13	0.08
Etrumeus teres vs. *Engraulis australis*	B	-0.06	0.86
Etrumeus teres vs. *Engraulis australis*	C	-0.06	0.81

4.3.3 Length frequency distributions

Patterns in the mean lengths of *S. sagax*, *E. teres* and *E. australis* larvae were examined for larvae collected at stations B and C. The mean lengths of most sardine larvae caught were between 2 and 10.5mm SL (Figure 4.6). Lowest mean lengths were found in spring and summer, with highest mean lengths found during winter. Mean lengths of *E. teres* were not as variable through the year, with mean lengths mostly between 3 and 6mm SL (Figure 4.6). Lowest mean lengths were found in late summer and spring with highest mean lengths in winter. Small *S. sagax* and *E teres* were thus found through the year. *Engraulis australis* larvae were generally smallest in spring and summer, coincident with the highest recorded concentrations (Figure

4.6). Highest mean lengths were found in winter, coincident with low larval concentrations.

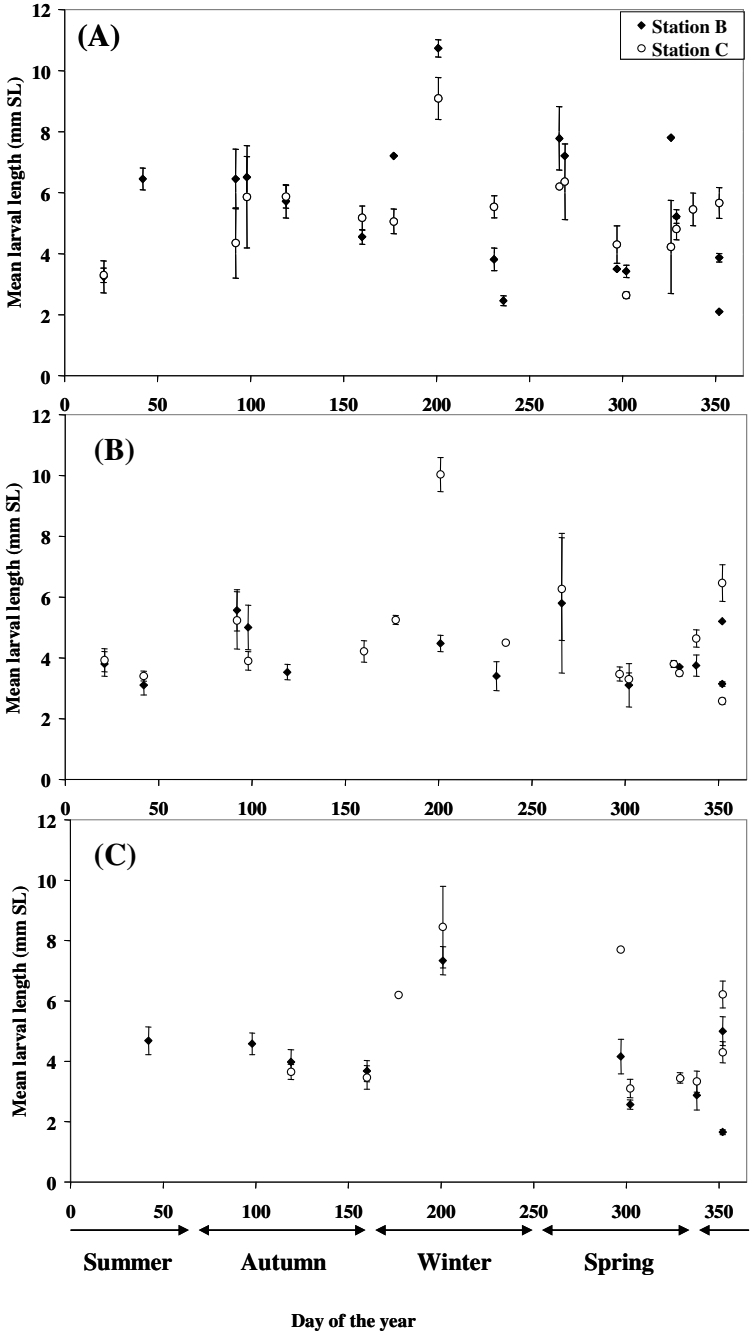

Figure 4.6: Mean length of (A) *Sardinops sagax,* (B) *Etrumeus teres and* (C) *Engraulis australis* larvae at stations B and C on the Two Rocks transect, with standard errors shown. Day of the year is shown on the x-axis, with data from two and a half years of sampling shown (August 2002 to December 2004).

4.3.4 Clupeiform spawning cycles

The monthly mean GSI of all adult *S. sagax* sampled from the Fremantle fishery over the six years 2000 to 2005 peaked in winter, especially in June, and was at a minimum in October and November (Figure 4.7).

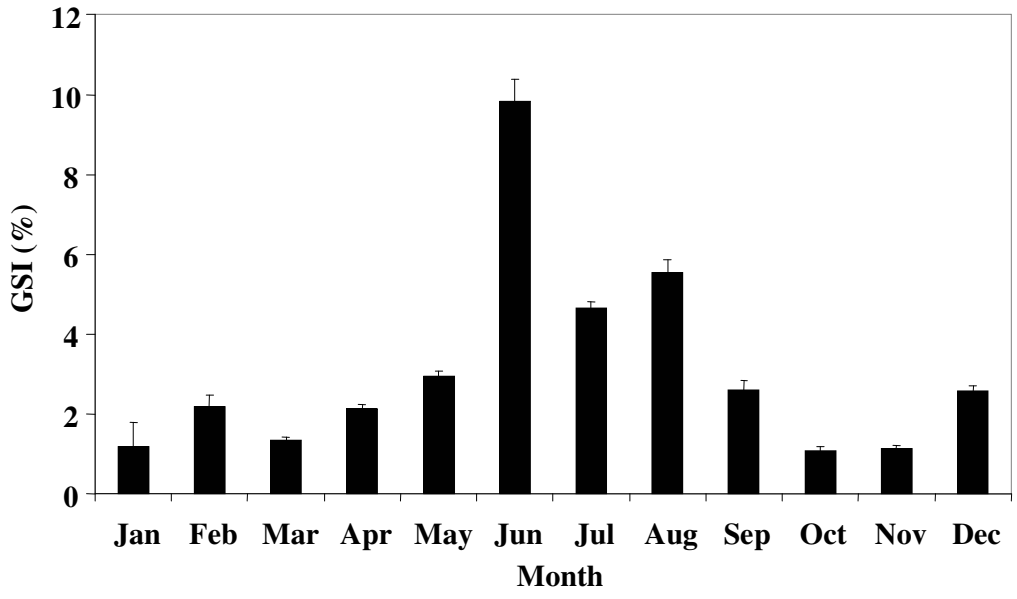

Figure 4.7: Six-year monthly mean of the gonadosomatic index of adult *Sardinops sagax*, caught by the Fremantle fishery in the Perth region. Data courtesy Department of Fisheries, Western Australia.

However, larval *S. sagax* concentrations at both station B, and Station C were not closely correlated to mean monthly GSI, across the sampled study period (Figure 4.8). Re-analysing the data incorporating a one-month lag between GSI and larval fish concentrations did not improve the correlation at either station (station B: R^2=0.08, station C: R^2=0.06). The poor correlations were largely due to low concentrations of larvae in June and July, coincident with high GSI (Figure 4.2).

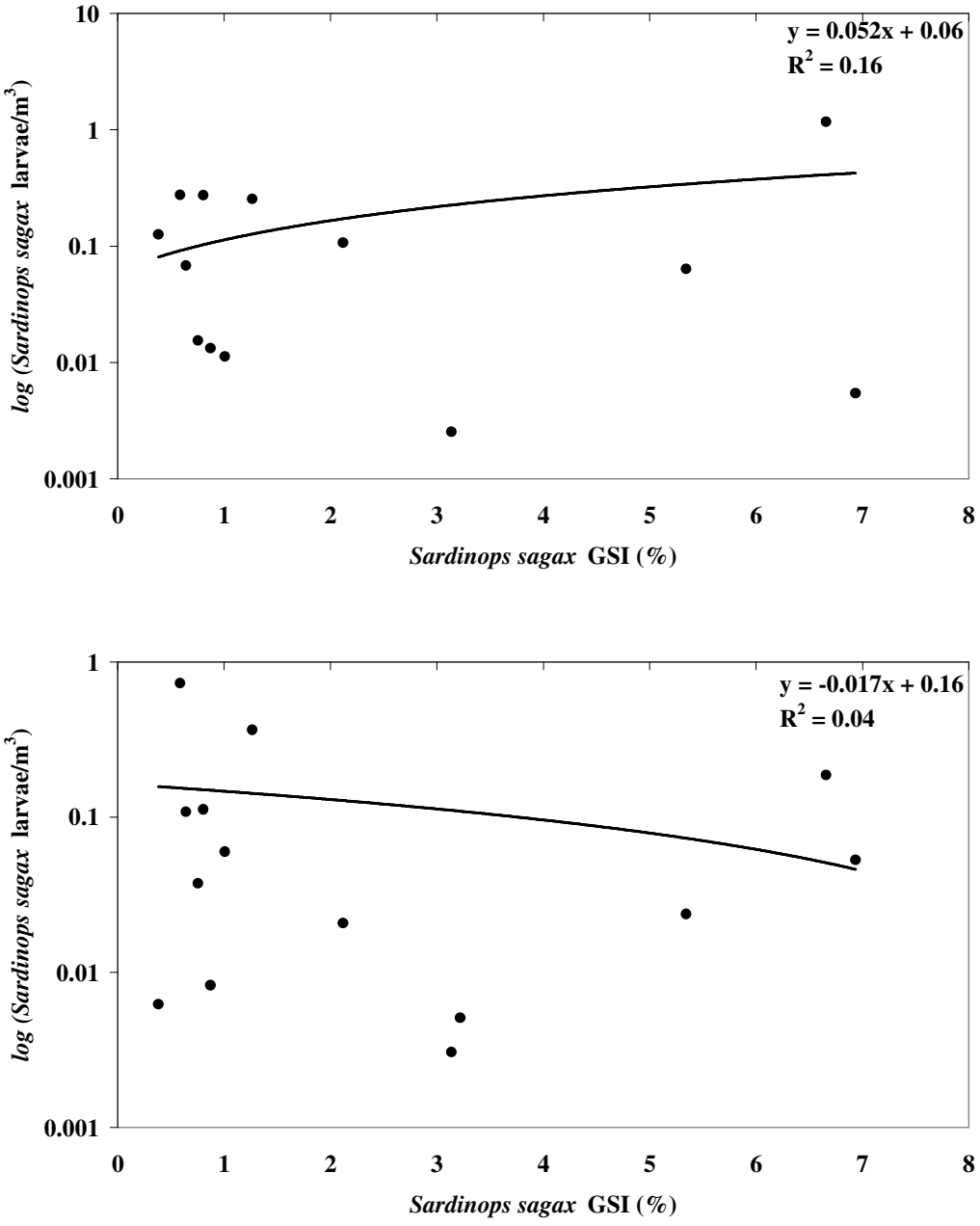

Figure 4.8: Scatterplots of mean monthly gonadosomatic index of adult *Sardinops sagax* collected in the Perth region, August 2002 to December 2004, and mean *S. sagax* larval abundance collected at station B (40m depth), and station C (100m depth) on the Two Rocks transect, August 2002 to December 2004. Larval fish concentrations are plotted on a logarithmic scale. GSI data courtesy Department of Fisheries, Western Australia.

4.3.5 Correlation of larval fish concentrations with environmental variables

To explore the influence of environmental variables on spatial and temporal patterns of *S. sagax*, *E. teres* and *E. australis* larvae, larval fish concentrations for each species were correlated to a selection of variables (Table 4.4). Larval concentrations of all three species showed significant correlations to environmental variables, with adjusted R^2 values of between 0.16 and 0.29. *Engraulis australis* concentrations showed the strongest correlations to environmental variables, with *E. teres* concentrations showing the weakest correlations, demonstrated by the lower R^2 statistics (Table 4.4).

Concentrations of all three species were correlated to microzooplankton concentrations, either at the surface or CM. The coefficients (b values) generated from the regression analyses were negative for microzooplankton concentrations, both at the surface and the CM, indicating that concentrations of larvae of all three clupeiform species were greatest when microzooplankton concentrations were lowest, i.e., a negative relationship. Concentrations of both *E. teres* and *E. australis* larvae were positively correlated with surface salinity, while concentrations of *S. sagax* larvae were positively correlated with surface chlorophyll α concentrations, but only in the presence of higher wind speeds and lower microzooplankton concentrations.

4.4 Discussion

4.4.1 Distribution patterns of clupeiform larvae

Sardinops sagax

Overall concentrations of larval *Sardinops sagax* in the current study were comparable with those found near Albany, on the south coast of Western Australia, by

Fletcher (1999), by Uehara *et al*. (2005), in the East Australian Current, by Beckley and Hewitson (1994) in the Agulhas Current, and also those found by Ward *et al*., (2006) on the open shelf off South Australia, but lower than concentrations found by the same authors around the more protected waters of Spencer Gulf, and around Kangaroo Island.

Table 4.4: Results of multiple linear regression analyses between a selection of environmental variables (see Table 4.2), and concentrations of *Sardinops sagax*, *Etrumeus teres*, and *Engraulis australis* larvae. "CM" denotes chlorophyll maximum layer.

Species included in analysis	Combination of environmental variables that best explained variation in larval fish concentrations. Coefficients (b) also shown
Sardinops sagax	Surface chlorophyll (b=0.44)
	Microzooplankton concentration at surface (b=-0.13)
	Microzooplankton concentration at CM (b=-0.0003)
	Wind speed (b=0.03)
	Adjusted R^2 = 0.24, p=0.01
Etrumeus teres	Salinity at surface (b=0.14)
	Microzooplankton concentration at surface (b=-0.05)
	Microzooplankton concentration at CM (b=-0.0002)
	Adjusted R^2 = 0.16, p=0.04
Engraulis australis	Day of the year (b=0.001)
	Wind speed (b=0.01)
	Salinity at surface (b=0.43)
	Microzooplankton concentration at surface (b=-0.10)
	FMSL (b=0.01)
	Adjusted R^2 = 0.29, p=0.01

However, concentrations of *S. sagax* in the current study were higher than concentrations found by Fletcher and Tregonning (1992), on the south coast of Western Australia, and also those found in the California Current in the 1980s and

1990s, by Smith and Moser (2003). Sardine concentrations along the Two Rocks transect were generally lower, however, than those found by Olivar *et al*. (2001), in the northwest Mediterranean, and by Huggett *et al*. (1998), and Stevenik *et al*. (2001) in the Benguela Current ecosystem.

Sardinops sagax spawns in shelf waters, at different times in different geographical locations (Ward *et al*., 2003), with larvae previously sampled in the Perth and Albany areas in high abundances in July and December (Gaughan *et al*., 1990; Neira *et al*., 1992; Kendrick, 1993; Fletcher *et al*., 1994). While spawning of *S. sagax* off South Australia has peaks at a particular time of year (January to April), in association with upwelling events (Ward and Staunton-Smith, 2002), GSI data suggests that spawning off Fremantle instead peaks in a time of strong southward Leeuwin Current flow (June to August), when there is no upwelling.

Gaughan *et al*. (submitted) found that across a transect off Hillarys (52km south of Two Rocks), <24 hour old *S. sagax* eggs showed highest concentrations in both winter and summer, on the inner shelf. These data, in combination with GSI and larval data, suggest that *S. sagax* spawns most of the year round, with peak spawning in winter, and some spawning activity in summer. However, some disparity was evident between *S. sagax* spawning times (as shown by GSI data), and larval concentrations in this study. In June and July, times of high GSI, very low concentrations of larval fishes were found. Given the spawning locations of *S. sagax* recorded by Gaughan *et al*. (2004), encompassing inner and outer shelf locations from Rottnest Island to Cape Leeuwin, and the strong Leeuwin Current flow along the shelf in June and July (as shown by FMSL data), it is possible that eggs and larvae resulting

from mid-winter spawning events would have been rapidly advected southwards (Caputi *et al*., 1996; Fandry *et al.,* 2006). This may have resulted in the very low concentrations of *S. sagax* larvae found at the shelf stations of the Two Rocks transect in June and July. Even if larvae were located inshore of the main influence of the Leeuwin Current, the bathymetry of the inshore waters in the vicinity of the Two Rocks transect results in strong southwards advection during winter (Fandry *et al*., 2006). The reason for high larval *S. sagax* concentrations in August, which is also subject to strong Leeuwin Current flow, (although not as strong as in June/July), may have related to either improved retention, or to the fact that the August cruises along the Two Rocks transect were both completed after major cold front events, with associated strong winds. Such storm events can result in increased onshore Ekman transport (Simpson, 1987), which may have resulted in the high concentrations (and/or catchability) of larvae around station B (see Chapter 3).

Spawning activity during summer may not be as high as during winter, however, it is likely that eggs and larvae would be better retained over the shelf, due to the presence of the Capes Current, which flows sporadically northwards over the shelf, at generally lower velocities than the Leeuwin Current (Gersbach *et al.,* 1999; Pearce and Pattiaratchi, 1999). Some offshore Ekman transport may be present in summer, especially at the surface (see Chapter 5), but it is proposed that retention conditions during summer would still be more advantageous than during winter. It is therefore possible that a comparatively short proportion of the sardine spawning period could produce the majority of the year's recruits to the adult population on the lower west coast of Western Australia. Given the seasonal and interannual variability in the

oceanography of the study region, a protracted spawning season may therefore be advantageous, to ensure that at least some eggs and larvae are retained.

Sardinops sagax larval concentrations were weakly correlated to a selection of environmental variables. Higher concentrations of larvae were associated with increased recent wind mixing, and with low concentrations of microzooplankton. This is an interesting result given that small zooplankton are an important component of the diets of larval *S. sagax* (Llanos *et al*., 1996; Uehara *et al*., 2005). Adult *S. sagax* have been shown to vary their spawning times and locations to allow their larvae to hatch into favourable feeding conditions (Ward *et al*., 2006; Ward *et al*., 2003; Hutchings *et al*., 2002; Somarakis *et al*., 2006). However, while spawning activity was high during times of high chlorophyll α and microzooplankton biomass, larval fish concentrations were not.

Etrumeus teres

Concentrations of *E. teres* were difficult to compare to those from other regions, as they were not as well recorded as for *S. sagax* or *Engraulis* spp., partially due to their lower commercial significance in most areas where they occur. However, concentrations of *E. teres* in this study were comparable to concentrations of *E. whiteheadi* found by Beckley and Hewitson (1994) in the Agulhas Current. *Etrumeus teres* larvae were found throughout the year on the continental shelf. Larvae of this species have been found previously along the east coast of Australia, off Brisbane and Sydney, at most times of year (Gray, 1995; Ward *et al*., 2003). *Etrumeus teres* larvae within the study area also showed evidence of a protracted spawning season, and similar spatial and temporal patterns in abundance to *S. sagax*, especially at station C.

It is therefore likely that the two species have similar spawning times and locations in and around the sampled area, and a similar response to some environmental variables. As with *S. sagax*, concentrations of *E. teres* were negatively, but weakly, correlated to microzooplankton concentrations. An association between the biology of *S. sagax* and *Etrumeus* spp. has been found previously off southern Africa (Beckley and Hewitson, 1994; van der Lingen *et al*., 1998). The extent of competition for food between *S. sagax* and *E. teres* larvae is unclear, but the slightly different vertical and horizontal distributions found between larvae of these two species in this study may be a mechanism by which this is avoided (see Chapter 5).

Engraulis australis

Concentrations of *Engraulis australis* in the current study were comparable with those of *S. sagax*. Concentrations of *E. australis* were also similar to those found in coastal waters off Perth by Kendrick (1993), and to those found off southern Queensland by Ward *et al.* (2003), but were lower than those found in Cockburn Sound, south-western Australia by Jonker (1993). Concentrations of *E. australis* in this study were also comparable to those of *E. encrasicolus* in the northwest Mediterranean (Olivar *et al*., 2001) and concentrations of *E. capensis* (now *E. encrasicolus)* in the Agulhas Current (Beckley and Hewitson, 1994), but lower than the concentrations of *E. mordax* found by Smith and Moser (2003), in the California Current region, and concentrations of *E. japonicus* found by Okazaki *et al.* (2002) in the Kuroshio Current region.

Highest concentrations of *Engraulis australis* larvae were found from spring to autumn on the continental shelf, often within the Capes Current. This was consistent

with the spring to autumn peak in spawning of this species reported previously (Gaughan *et al*., 1990; Neira *et al*., 1992). High concentrations of *E. australis* larvae were recorded together with high concentrations of larvae from the Monacanthidae and Labridae, as well as those from the Triperygiidae and *Creedia haswellii*, suggesting that *E. australis* larvae were associated with water of a more inshore origin than the one containing high concentrations of *S. sagax* (see Chapter 2). Unlike *S. sagax* and *E. teres*, *E. australis* larvae were also found consistently, although in low numbers, at station A. *Engraulis australis* usually spawns closer to shore than *S. sagax*, and is better able to tolerate the high water temperatures, and high salinities found in shallow coastal and estuarine environments in summer (Ward and Staunton-Smith, 2002; Dimmlich *et al*., 2004).

Larvae of *Engraulis* spp. in other parts of the world are found in association with warm, stratified water columns, and/or in association with the seasonal minimum in deleterious offshore transport (Lasker, 1975; Bergeron, 2000; Olivar *et al*., 2001). The inner shelf off south-western Australia in summer provides warm, stratified conditions, and was associated with higher concentrations of *E. australis* larvae. The negative correlation between microzooplankton at the surface, and *E. australis* larvae suggests that the well-mixed conditions that generally result in higher abundance of microzooplankton were not associated with higher concentrations of *E. australis* larvae. The positive correlation between surface salinity and *E. australis* larvae reflected their tendency to be located within higher salinity water masses such as the Capes Current, and summer inshore water. In contrast, samples which contained high abundances of *S. sagax* larvae were often found in winter and spring, when wind mixing was higher, and the water column less stratified (see Chapters 2 and 3).

Spratelloides robustus

The only other Clupeid species found in the larval fish samples was *Spratelloides robustus*. This species is endemic to Australian waters, and adults mostly occupy sheltered nearshore areas (Rogers *et al*., 2003). Larval *S. robustus* were only found inshore, and in summer. Unlike *S. sagax*, *E. teres* or *E. australis*, *S. robustus* has demersal eggs (Rogers *et al*., 2003), which was likely to have resulted in the observed inshore distribution (Suthers and Frank, 1991). This species has been reported to spawn in a single season, from spring to summer (Neira and Potter, 1992; Gray, 1995; Rogers *et al*., 2003).

4.4.2 Implications for fisheries

Biomass and commercial catches of clupeiform fishes off south-western Australia, such as sardine and anchovy, are insignificant by world standards, especially in comparison to other southern hemisphere eastern boundary currents (Lenanton *et al.,* 1991). Part of the reason for this may be explained by the oligotrophic nature of south-western Australian waters (Pearce *et al*., 2000; Hanson *et al*., 2005), which may result in lower secondary production (Koslow *et al*., 2005), and therefore less food for pelagic larvae. However, it would appear that this effect is compounded by the fact that the time of greatest primary productivity off the south-western Australian coast (autumn/winter) (Lourey *et al*., 2006) occurs at a time of potentially unfavourable southward transport for shelf spawning species. Clupeiod larvae are generally poor swimmers (Froese, 1990, Fisher *et al*., 2005); their reproductive strategy instead focuses on spawning throughout the year, so that larvae hatched during times of favourable retention may survive (Hutchings *et al.,* 2002; Rogers *et al*., 2003). This

may not be an effective strategy in Western Australian waters, given the biological oceanography.

This is in contrast to the situation off South Australia, for example, where coastal upwelling in summer and autumn is associated with increased primary production, increased zooplankton biomass, and high concentrations of *S. sagax* eggs and larvae (Ward *et al*., 2006). Favourable feeding and growth conditions for larvae therefore occur in conjunction with potentially favourable larval retention conditions (Herzfeld and Tomczak, 1997; Ward and Staunton-Smith, 2002; McClatchie *et al.,* 2005). This results in the spawning biomass of *S. sagax* in waters off South Australia being an order of magnitude higher than elsewhere in southern Australia (although still much lower than populations associated with upwelling eastern boundary currents) (Ward *et al*., 2006).

Bakun (1996) proposed three major classes of physical processes that characterise favourable reproductive habitats for coastal pelagic fishes, such as clupeiform species. These were enrichment processes (e.g., upwelling), concentration processes (e.g., fronts, and stable water columns), and retention mechanisms. Low catches of clupeiform species off south-western Australia are usually ascribed to the low nutrient and chlorophyll biomass concentrations present in shelf waters, as a result of the suppression of upwelling by the Leeuwin Current (Pearce, 1991; Hanson *et al*., 2005). However, examination of the three criteria proposed by Bakun (1996) would suggest that south-western Australian waters are largely devoid of all three mechanisms. There is no large-scale upwelling, few concentration processes, with no strong

hydrographic fronts usually present, and a lack of retention mechanisms for pelagic, shelf-spawned larvae during times of higher productivity (i.e., autumn and winter).

Rates of predation on clupeiform larvae off south-western Australia are currently unknown, but may be assumed to be high for smaller, slower-growing larvae which do not encounter favourable food patches (Bailey and Houde, 1989). A combination of these factors may therefore be responsible for low clupeiform stock sizes and catches off south-western Australia.

Retention conditions on the continental shelf in the vicinity of the sampled transect in autumn and winter are particularly poor. Larvae entrained within the Leeuwin Current during autumn or winter may be transported southwards by up to 40km per day (assuming passive transport) (Cresswell, 1991), or 20km a day inshore of the main current, as it extends inshore over the shelf (Caputi *et al*., 1996), with no apparent mechanism existing for larval retention close to spawning areas on the open continental shelf. It would therefore appear that the southward transport mechanism present during winter would quickly advect shelf-dwelling pelagic larvae away from spawning locations, within the area studied. The apparent existence of separate *S. sagax* stocks between the west and south coasts of Western Australia (Gaughan *et al*., 2001c,) suggests that larvae entrained within the Leeuwin Current are not usually recruited to south coast stocks. However, small *S. sagax* are reportedly common in the comparatively protected waters of Geographe Bay, located approximately 250km south of the sampled transect, between Cape Naturaliste and Mandurah (south of Perth). Recruitment of larvae spawned on the open shelf around Two Rocks and Perth to Geographe Bay is therefore possible (Gaughan *et al*., 2001c).

Recruitment to the sardine fishery off south-western Australia has been negatively correlated to Leeuwin Current flow two years previously (Caputi *et al*., 1996). Strong Leeuwin Current flow has been linked to higher phytoplankton biomass (Koslow *et al.*, 2005), and nutrient and chlorophyll concentrations generally peak during winter in the study region (Lourey *et al*., 2006). Therefore, it is likely that the negative influence of the Leeuwin Current on the sardine fishery is largely related to advective processes, rather than food limitation only.

This conclusion is supported by the recent determination of larval *S. sagax* growth rates, using larvae collected from the Two Rocks transect (Jones, 2006). Growth rates of these larvae were found to be comparable to, or higher than, those in other, more productive parts of the world. This may be a result of the higher water temperatures provided by the Leeuwin Current. It is possible that such fast growing larvae would suffer high rates of mortality in an oligotrophic environment. However, the effect of deleterious advection processes has also been noted in the Agulhas and Benguela Current systems off southern Africa, where despite high primary productivity, yields of pelagic fishes are lower than in the Humboldt system off South America. It has been suggested that this is partly due to the poor retention conditions present for pelagic larvae along the southern African coast, as a result of the strong western boundary current (Agulhas Current), and the strong upwelling environment present off the west coast, which may result in considerable offshore losses of pelagic eggs and larvae (Hutchings *et al*., 1998, 2002).

4.5 Conclusions

Clupeiform larvae were found to be ubiquitous on the shelf off south-western Australia throughout the study period, with concentrations of most species highly variable between months and between years. However, interannual patterns of variability were difficult to determine, given the limited spatial resolution of sampling along a single transect. *Sardinops sagax* and *E. teres* larvae were present throughout the year, with high concentrations of these larvae associated with low concentrations of some potential prey items, such as microzooplankton. It is suggested that the presence of unsuitable southward transport conditions for larvae during the time of highest phytoplankton and zooplankton biomass (autumn/winter) resulted in the negative correlations observed. These conclusions support the findings of similar studies on the south coast, which suggest potentially poor retention for *S. sagax* larvae during time of strong Leeuwin Current flow. *Engraulis australis* larvae were most common from spring to autumn, and were mostly found inshore of *Sardinops sagax* larvae. *Spratelloides robustus* larvae were uncommon, and found only at stations A and B in spring and summer. This was likely due to this species having benthic eggs, and a less protracted spawning season than the other species sampled.

Chapter 5: Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport

5.1 Introduction

Pelagic eggs and larvae of many fish species may be dispersed over large areas of ocean, by a variety of mechanisms. The ability of fish larvae to survive this pelagic phase, and remain in, or return to, a suitable habitat for settlement and metamorphosis may be dependent on their ability to regulate their dispersal or retention (Heath, 1992; Urho, 1999; Cowen, 2002).

Physical oceanographic processes are highly influential in regulating the distribution of fish eggs and larvae, and affect distribution on a variety of scales, ranging from a few metres to thousands of kilometres (Bruce *et al.,* 2001). The distribution of some taxa can be related to specific oceanographic features, with variations in the location of such features having implications for larval fish survival and recruitment (Doyle *et al.*, 1993). The most obvious of such features with regard to larval dispersal are the major ocean current systems, with the eddies, jets and gyres associated with these currents also influential (e.g., Logerwell *et al*., 2001; Hare *et al*., 2001, 2002). Some coasts are also characterised by the presence of upwelling or downwelling features, which affect both the retention of larvae, and the concentration of prey items available to them (Rodriguez *et al*., 1999; Santos *et al.*, 2004). Smaller scale processes, however, such as the formation of coastal and tidal fronts, are also important in some regions (Grioche and Koubbi, 1997; Sanvicente-Anorve *et al*., 2000). The

magnitude and direction of larval fish transport by ocean currents varies temporally and spatially, as the current strength and position varies in response to climatic processes. Some fish species in areas with strongly seasonal oceanographic features have been found to adapt their spawning times and locations to take advantage of favourable transport mechanisms for their larvae, and to avoid times where disadvantageous mechanisms prevail, such as strong offshore Ekman transport (Parrish *et al*., 1981; Sinclair, 1988; Hutchings *et al.,* 2002). The structure of the larval fish assemblage within a region will therefore be influenced by the seasonal patterns of spawning by different species, and the presence and strength of the oceanographic processes with which spawning times coincide.

As the strength and flow direction of many currents differ with respect to depth through the water column, the ability of a larva to vertically position itself is a mechanism by which a favourable horizontal position may be achieved or maintained (Heath, 1992). Larval fish assemblages are therefore maintained by a combination of physical features, and larval behaviour. Larvae of different species differ in their response to the physical environment, and some larvae appear to utilise transport processes that others do not (Cowen *et al*., 2003; Hare and Govoni, 2005). As larvae develop fins, and swimming abilities, they possess the potential for significant horizontal, as well as vertical movements. Armsworth (2001) concluded that physical processes, and passive entrainment were less important in determining positioning of larvae of reef fish, than consideration of larval swimming. Therefore, while larval fish assemblages may be well-aligned to oceanographic boundaries on a regional scale, fine-scale processes and larval fish

behaviour are also potentially important in structuring assemblages on a more local scale: the scale at which most larval fish sampling is carried out (hundreds of metres).

Larval fish may position themselves vertically in the water column to align themselves with a particular physical or biological feature. In stratified water columns, some studies have found greatest concentrations of larval fishes in and above the thermocline (Ahlstrom, 1959, Kendall and Naplin, 1981). Larvae have also been found to aggregate vertically around the layer of maximum prey concentration, or the chlorophyll maximum layer (Matsuura *et al*., 1993; Groenkjaer and Wieland, 1997). However, other studies have found that the selection of specific depth distributions by different species, independent of physical and biological structures in the water column, were more important in determining vertical assemblage structure (Leis, 1982; Gray, 1996; Cowen *et al.,* 2003), especially in oceanographically dynamic regions. The selection of a specific depth range by larvae may also allow them to concentrate in areas where food particles are most abundant, or where predators are least abundant (Heath, 1992). However, as with responses to physical gradients, strategies and behaviours among taxa are not uniform, with different species in the same area often showing different behaviours and responses. Additionally, the selection of depth ranges by larvae may change with growth, with many species shown to change behaviours as they age (Leis, 1982, 1991; Smith, 2000).

Many species also show a change in their vertical distribution between day and night: diel vertical migration (Kendall and Naplin, 1981; Brewer and Kleppel, 1986). This

behaviour may be related to feeding behaviour or predator avoidance (Kendall and Naplin, 1981). The vertical structure of a larval fish assemblage at any location, therefore, will be a product of the presence of oceanographic dispersal mechanisms, the distribution of larval prey items, time of day, and the response of larvae from different species and age cohorts to these features.

This study aimed to compare the vertical and horizontal structure of larval fish assemblages between summer and winter sampling cruises, and to relate larval fish assemblage patterns to regional oceanographic and biological processes. It was hypothesized that the larval fish assemblage structure would mirror the distinctive oceanographic conditions found during each season, and that vertical depth distributions of larvae would affect their horizontal position. Taxon-specific differences in vertical position were examined for both seasons, and implications for the resulting dispersal or retention of larvae are discussed.

5.2 Materials and methods

5.2.1 Larval fish sampling

Two nine day cruises aboard the *RV Southern Surveyor* were undertaken off south-western Australia in August 2003 (winter), and January 2004 (summer). Four of the five stations across the Two Rocks transect were occupied: station B (40m depth, inner shelf), station C (100m depth, outer shelf), station D (300m depth, shelf break) and station E (1000m, offshore) (see Chapter 2).

Multiple CTD, zooplankton and primary productivity samples were taken from each station over the cruise period (Koslow *et al.*, 2005). Plankton samples were taken with

a multiple opening and closing EZ net, fitted with 335µm mesh (mouth area 1.0m^2), that could be deployed to sample specific depth strata. The maximum depth stratum sampled in this study was to 300m. A flowmeter positioned in front of the net was used to calculate the volume of seawater sampled by each net on each tow. EZ nets were used to sample depth strata as shown in Table 5.1. The net was towed at a speed of approximately 2 knots, with sampling taking place during both day and night. There were no net deployments in summer at stations B and E during the day, due to equipment failure.

For statistical analyses of horizontal patterns in larval fish concentrations and assemblage distributions, data from the un-replicated EZ net tows were supplemented with data from replicated, oblique bongo net tows, fitted with 355mm mesh (mouth area 0.196m^2), taken at the same sampling stations (B to E) during the day only, towed to 150m depth, or just above the bottom in shallower water (Table 5.1). Plankton samples from both nets were fixed in 10% buffered formalin immediately after collection. Larval fish were removed from plankton samples with the aid of a dissecting microscope. Where samples contained a very large amount of plankton, they were split using a Folsom splitter, and half the sample only was sorted (shown in italics in Table 5.1). Larval fish abundances from these samples were then multiplied by two to obtain an estimate of larval fish concentration (number per m^3). Fish larvae were preserved in 70% ethanol after sorting, and identified to family, and species where possible, using relevant literature (e.g., Leis and Carson-Ewart, 2000; Neira *et al.*, 1998). Larval fish concentrations (number/m^3 of seawater sampled) were determined using the flowmeters fitted to both net types, with mean concentrations and standard errors calculated for replicated tows.

Table 5.1: Depth strata sampled by the EZ net on the Two Rocks transect: winter vs. summer. Samples where only half the sample was sorted, due to a very high volume of plankton, are indicated in italics.

Station	EZ net depths sampled in August 2003 (winter).	EZ net depths sampled in January 2004 (summer).	Bongo net samples taken: August 2003 and January 2004.
B (40m)	0-10m, *10-20m*, *20-30m* (day) *0-8m, 8-20m, 20-30m* (night)	No deployment during the day *0-9m, 9-20m*, 20-30m (night)	Two replicated tows from just above the bottom.
C (100m)	*0-25m*, 25-50m, 50-75m (day) *0-25m, 25-50m, 50-75m* (night)	0-30m, 30-65m, 65-85m (day) 0-30m, 30-55m, 55-80m (night)	Two replicated tows from just above the bottom.
D (300m)	*0-30m, 30-70m*, 70-120m (day) *0-30m, 30-70m*, 70-120m, 120-230m (night)	0-30m, 30-80m, 80-120m, 120-150m, 150-200m (day) 0-30m, 30-80m, 80-120m, 120-150m, 150-200m (night)	Two replicated tows from 150m depth.
E (1000m)	0-30m, 30-80m, 80-150m (day) 0-30m, 30-70m, 70-150m (night)	No deployment during the day 0-30m, 30-65m, 65-90m, 90-150m, 150-300m (night)	Two replicated tows from 150m depth.

5.2.2 Oceanographic data

Sea-surface temperature data were acquired from the Western Australian Satellite Technology and Applications Consortium (WASTAC), and the images were

processed by CSIRO Marine Research at Floreat, Western Australia. Temperature, salinity and chlorophyll α data were obtained from CTD casts taken on each cruise at each station, B to E (see Chapter 2). Chlorophyll α biomass data were derived from fluorescence measurements during CTD casts, using a regression equation determined after consideration of data from three years of sampling in the area (Koslow *et al.*, 2005). Temperature and salinity data were used to construct TS plots for each cruise, with data from the upper 150m of the water column used, or from the whole water column for shallower stations. CTD casts taken between stations were also used to construct temperature and chlorophyll profiles across the transect for each cruise, in order to improve spatial resolution. Spatial data for all profiles were gridded using the nearest neighbour method, in the Surfer-6 computer program. The position of the thermocline was defined as the zone of greatest change in temperature though the water column.

Current profiles with depth were obtained for January 2004 only, from a hull mounted ADCP (Acoustic Doppler Current Profiler). East-west, and north-south component data were taken for the duration of the cruise, and later averaged into 20-minute profiles. By subtracting the east-west and north-south components of the ship's speed from the relative components measured by the ADCP, absolute east-west and north-south current components were calculated through the water column. Profiles were extracted for each of the four sampling stations, with data binned every 8m, with the shallowest mean depth shown being 16.8m.

5.2.3 Data analyses

Larval fish concentrations were compared between seasons, and between sampling zones using the replicated bongo net tows. For these analyses, data from stations B and C were combined as "shelf" data, while data from stations D and E were combined to give "offshore" data, as too few samples were taken to compare larval fish between each station within each cruise. The Mann-Whitney test, in SPSS 14.0, was used for all tests for differences in mean larval fish concentrations between seasons, or between sampling zones within seasons. Profiles created in Surfer-6 displayed depth-stratified EZ net larval fish concentrations, which were plotted at the median depth for each stratum sampled. Larval fish concentration profiles from EZ net data examined night data only.

Vertical and horizontal distributions of the six most abundant larval fish taxa were examined and compared using both bongo net and EZ net data. The changes in horizontal and vertical position of larvae relative to their size (mm SL) were also investigated for *Sardinops sagax* (Clupeidae), *Etrumeus teres* (Clupeidae) and Tripterygiidae larvae, for summer EZ night samples only. Horizontal differences were tested statistically using the Mann-Whitney test.

Assemblage structure was investigated using the Primer-6 software package (Clarke and Warwick, 2005). To reduce the weighting of dominant species, larval fish concentration values were $\log_{(x+1)}$ transformed prior to analysis. Differences between larval fish assemblages from between seasons, and between shelf and offshore station groupings within each season, were investigated using analysis of similarity (ANOSIM), also in Primer-6. Assemblages collected between tow types were also

tested using ANOSIM, as were differences between day and night samples from the EZ net, to validate combining these samples for later assemblage analyses.

The similarity percentage routine SIMPER (Clarke and Warwick, 2005) was applied to the data to identify species characteristic of the assemblages from each zone (shelf or offshore) of each season (summer or winter), and also those species responsible for distinguishing between assemblages. Taxa that distinguished assemblages from the same zone, between summer and winter samples, were also identified, using a ratio of the mean contribution of any one species to the overall dissimilarity between samples groups ($\overline{\delta}_i$), to the standard deviation of $\overline{\delta}_i$ values from all constituent species [SD($\overline{\delta}_i$)] (see Chapter 2) (Clarke and Warwick, 2001). Day and night samples from bongo and EZ net samples were combined for these analyses, with EZ net samples integrated to the same sampling depth as the bongo nets.

5.3 Results

5.3.1 Oceanographic conditions

During the winter 2003 cruise, the warm, poleward-flowing Leeuwin Current was the dominant feature, covering stations B, C and D across the transect (Figure 5.1). Station E was west of the outer edge of the Leeuwin Current, in the cooler Sub-tropical Surface Water (STSW) (as defined by Woo *et al*., submitted). During the January 2004 cruise, the Leeuwin Current was much weaker than in August (Koslow *et al.*, 2005), and temperature differentiation across the transect was also weaker (Figure 5.1).

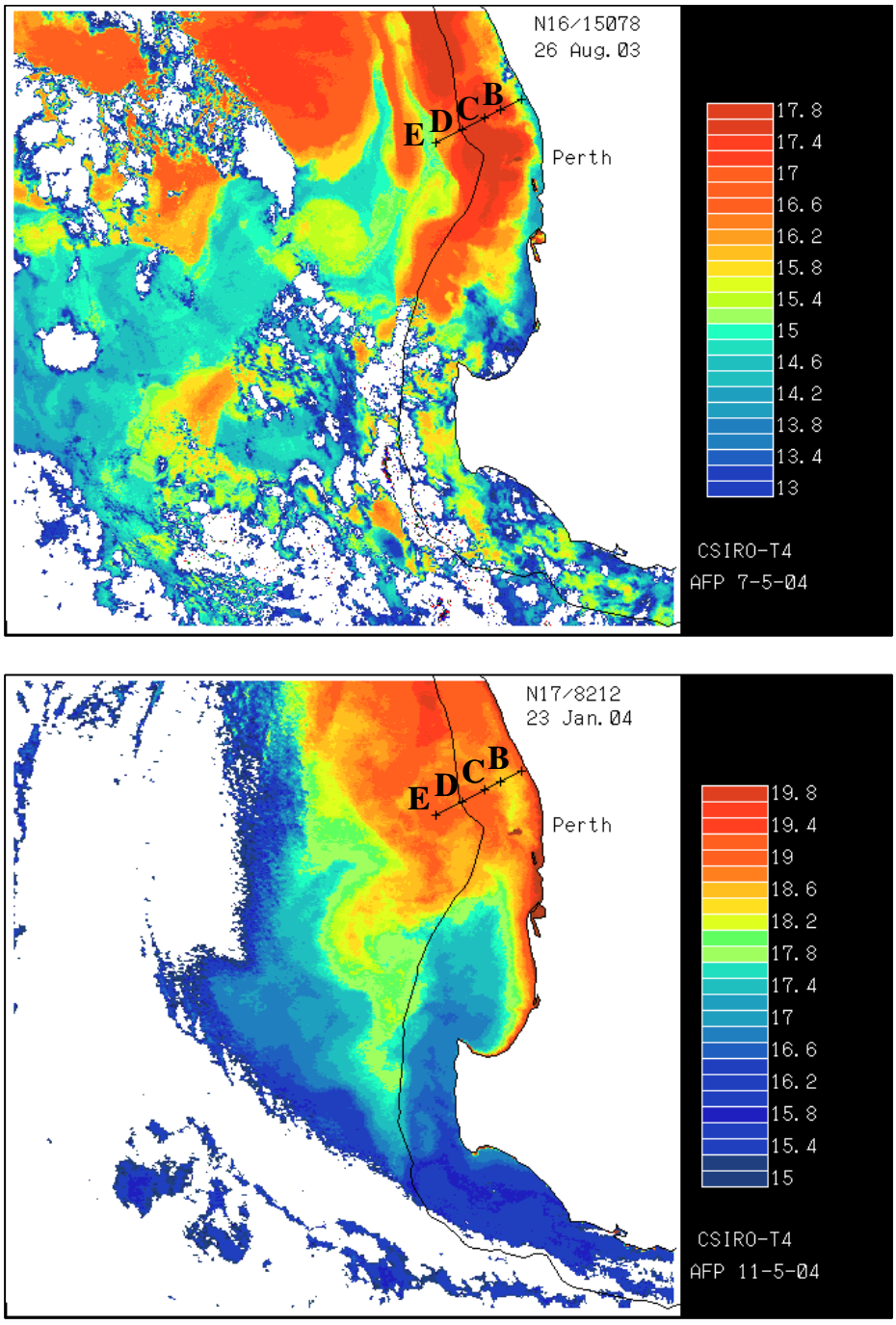

Figure 5.1: Sea surface temperature (brightness temperature) images of the Leeuwin Current derived from the Advanced Very High Resolution Radiometer (AVHRR) Band 4 on the NOAA-16 and -17 satellites. The warmest water (Leeuwin Current) is shown in red and the coolest water in blue, and white mottled regions are clouds. The black line is the 200 m isobath, approximating the continental shelf break. The study transect, and sampled stations, are shown. Images courtesy of WASTAC.

Station B appeared to be affected by the cooler upwelling wake that results from the Capes Current flowing northwards past Rottnest Island. Stations C, D and E were located within water of Leeuwin Current origin.

Temperature and salinity (TS) plots were examined for each station on each cruise, to compare the water masses present. In winter, stations B, C and D were situated in comparatively warm water (up to 19.7°C), indicative of their position in the Leeuwin Current (Figure 5.2). Cooler temperatures at station E indicated that this station was situated beyond the boundary of the Leeuwin Current, in STSW. Station B was warm and saline in summer, while stations C, D and E showed very similar water mass properties to each other during this cruise.

Profiles of both temperature and chlorophyll α biomass were used to compare water mass properties across the whole transect for both cruises. In the winter cruise profile, the warm Leeuwin Current was clearly evident in the temperature profile, as a mass of warm water situated against the shelf break (Figure 5.3). Downwelling was evident along the outer shelf and slope. The water mass inshore of this feature was relatively cool (17-18°C). In the summer profile, there was less distinction with temperature across the transect, although the Leeuwin Current was still present over the outer shelf and slope, as a shallower layer of warm water. The slope of the isotherms suggests some cryptic upwelling may have been present along the slope in summer, although this did not reach above 150m depth (Figure 5.3).

Chlorophyll α biomass was higher across the shelf in winter (Figure 5.4). The chlorophyll maximum layer within the water column tended to be at a shallower depth

in winter, and was more clearly defined. Chlorophyll α biomass in winter was particularly high on the shelf, around station B. In summer, there was a deeper, more diffuse chlorophyll maximum layer, at around 100m depth, with a slight increase near the surface at the shelf break.

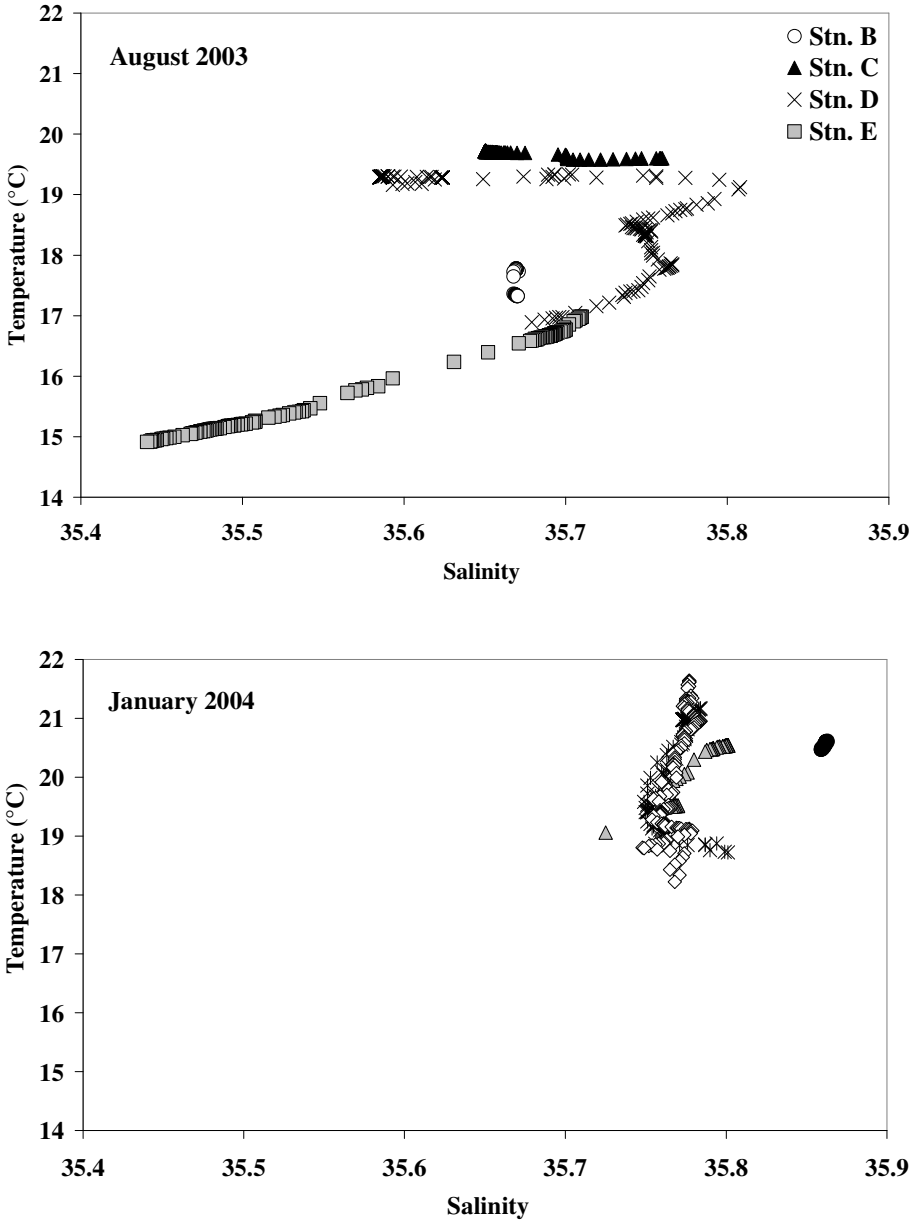

Figure 5.2: Temperature/salinity plots for four stations (B to E), sampled across the Two Rocks transect during August 2003 and January 2004. Data are shown for the upper 150m of the water column, or to just above the bottom in shallower water.

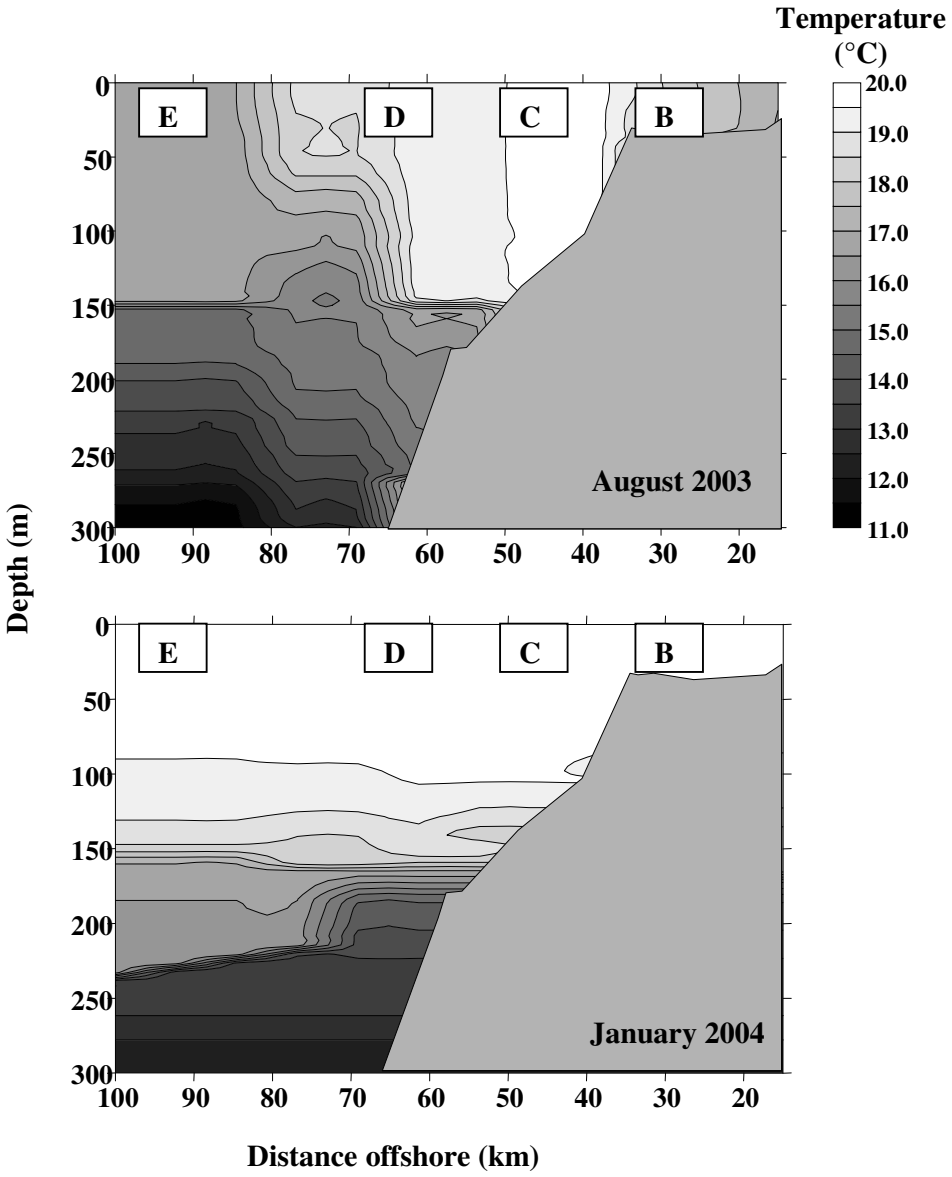

Figure 5.3: Temperature sections across the Two Rocks transect off south-western Australia: August 2003 and January 2004.

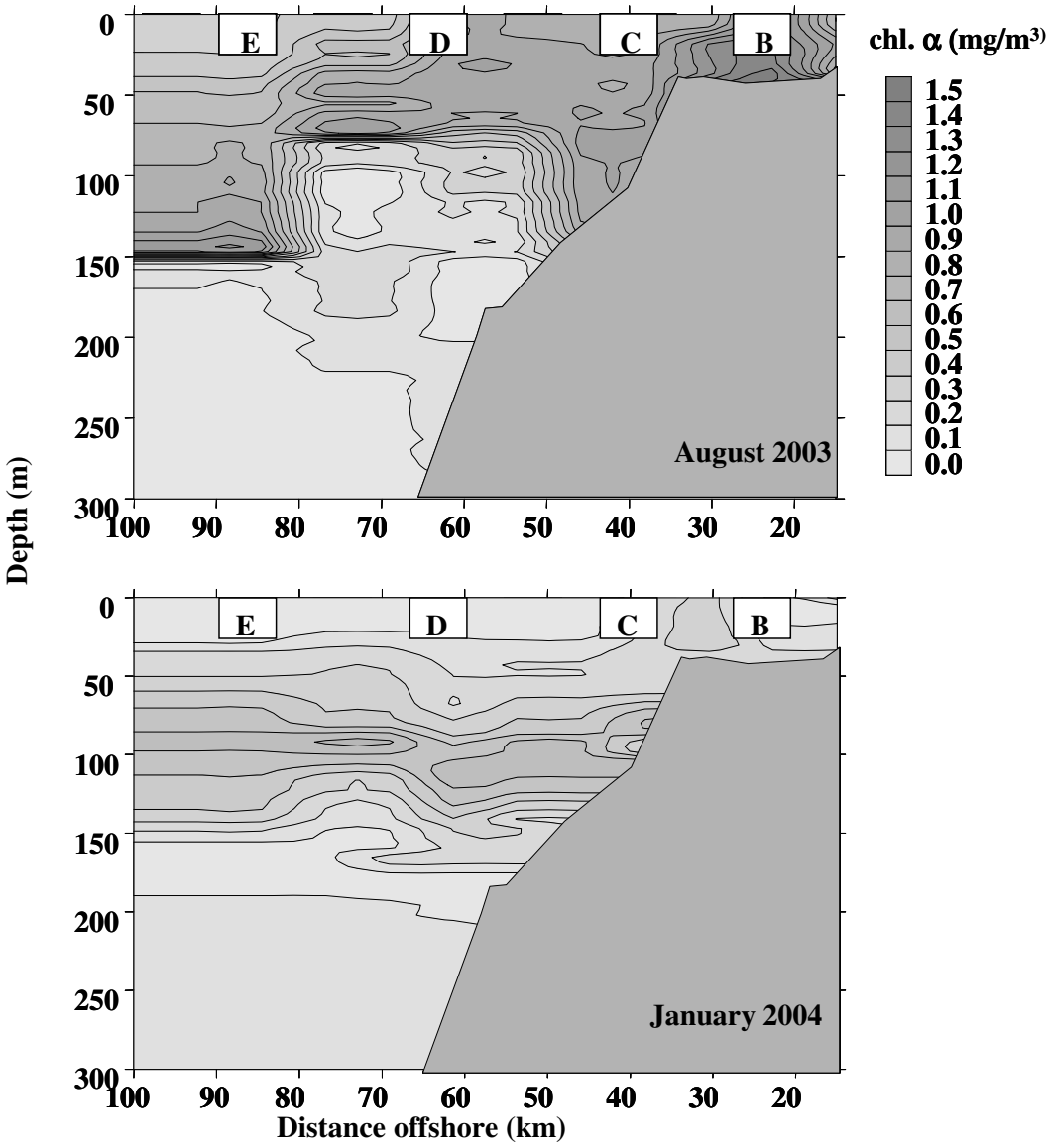

Figure 5.4: Chlorophyll-α biomass sections across the Two Rocks transect off south-western Australia, August 2003 and January 2004.

ADCP data from January 2004 supported the interpretation of sea-surface temperature satellite data and TS data. Currents at station B were flowing to the north-west at 0.1 to 0.2 m/s (Figure 5.5).

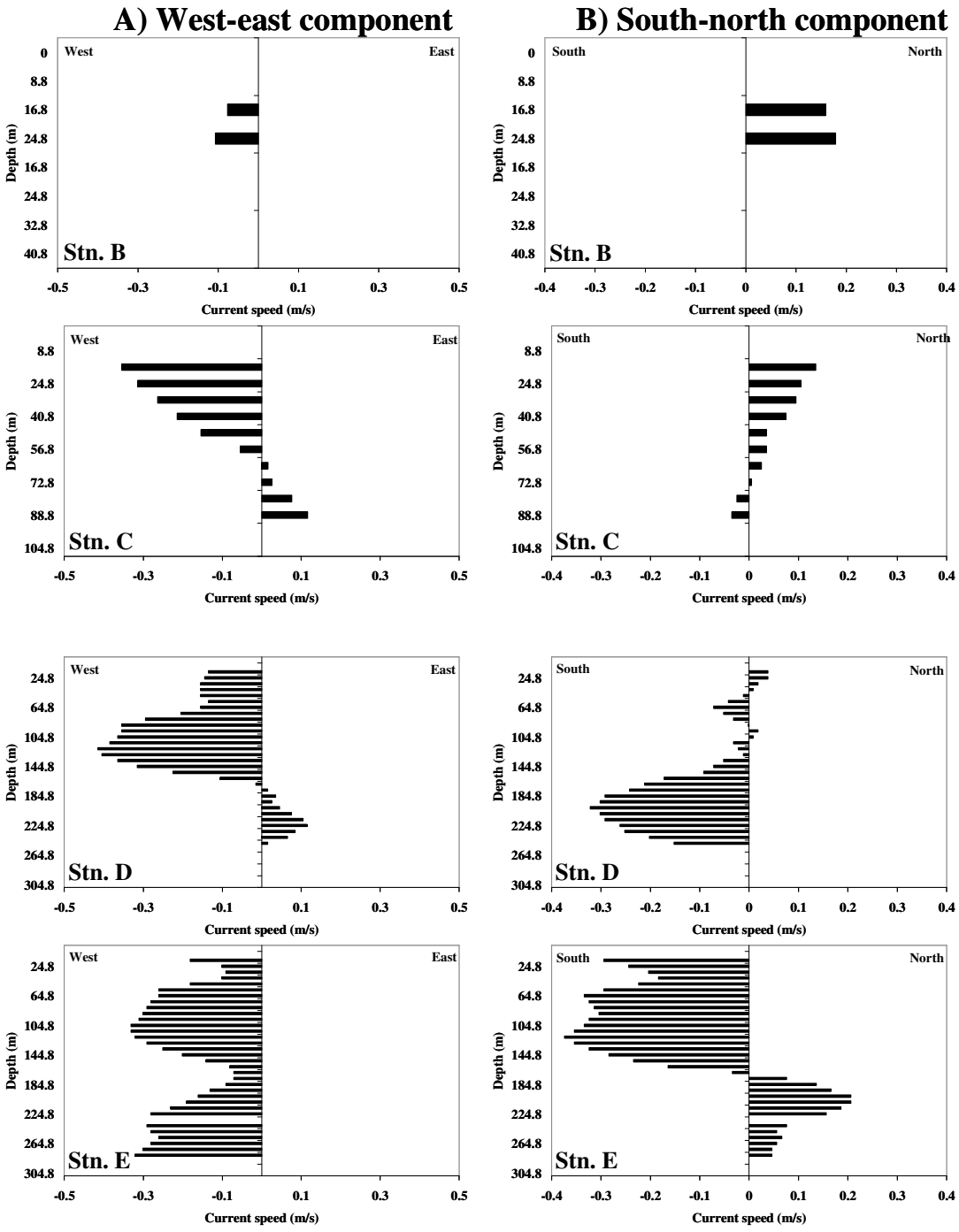

Figure 5.5: ADCP data for January 2004, on the Two Rocks transect: A) West-East component, B) South-North component. Twenty minute-averaged data are shown every 8m depth bin for stations B (40m) C (100m), D (300m) and E (1000m). Available data shown for the depth of the water column at each station, except for station E, where only the top 300m is shown.

Current profiles from station C showed changes in the current profile with depth. At the top of the water column, the currents were to the north-west, similar to station B, but with a stronger westward component (0.35m/s). However, this current weakened, and reversed, with depth through the water column, approaching zero between 60 and 70m depth, and then flowing weakly to the south-east near the bottom (0.12m/s). Station D also showed a westward current component at shallower depths, with current speeds peaking at around 112m (0.42m/s). Below 160m depth at station D, the current flowed strongly southwards, with speeds peaking at 190m depth (0.32m/s). The current at station E flowed to the south-west above 170m depth, below which it flowed to the north-west.

5.3.2 Taxonomic composition of assemblages.

A total of 5 713 fish larvae were identified from all plankton samples taken: 4 657 from the EZ net tows (1 726 from winter and 2 931 from summer), and 1 056 from the bongo net tows (425 from winter and 631 from summer). Larvae from 59 teleost families, and 107 identifiable taxa were recorded (Table 5.2). The winter shelf and offshore samples both contained a total of 52 taxa, with the summer shelf samples containing 55 taxa, and the summer offshore samples 46 taxa.

There were pronounced differences in dominant species between summer and winter samples (Table 5.2). Some taxa, such as *Apogonops anomalous*, *Etrumeus teres* and *Diaphus* 'slender' spp. were much more abundant in summer, whereas Clinidae sp. 1, *Scopelopsis multipunctatus* and *Cyclothone* spp. were more abundant in winter. Other taxa, such as *Diogenichthys atlanticus* and *Vinciguerria* spp., were abundant at both sampling times.

Table 5.2: Concentration (number/1000m^3) of all larval fishes collected at stations B-E in the EZ nets only, winter and summer. Note: no day samples were taken at stations B and E in summer.

Family	Species	Winter				Summer			
		Station B (mean #/m^3)	Station C (mean #/m^3)	Station D (mean #/m^3)	Station E (mean #/m^3)	Station B (mean #/m^3)	Station C (mean #/m^3)	Station D (mean #/m^3)	Station E (mean #/m^3)
Acropomatidae	*Apogonops anomalous*						35.77	5.29	2.59
Apogonidae	Apogonidae sp. 1	0.58							
Blenniidae	*Parablennius postoculomaculatus*	2.48				13.10			
Bregmacerotidae	*Bregmaceros* sp.		3.69	6.73				2.05	
Callanthidae	*Callanthius* sp. 1		2.63						
Callionymidae	Callionymidae sp. 1	15.02	4.01	0.63			24.27	0.42	
Carangidae	Carangidae spp.	3.06	0.62			37.04	143.46	4.64	0.27
	Pseudocaranx spp.						2.12		
	Trachurus novazelandiae								6.26
	Seriola sp. 1								0.27
Ceratoidea	Ceratoidea sp. 1			1.11					
Chaetodontidae	Chaetodontidae sp. 1				0.25				
Chauliodontidae	*Chauliodus sloani*		3.69	6.45	0.68				
Chiasmodontidae	*Kali macrura*		0.92	2.89					
Clinidae	Clinidae sp. 1	17.01	3.11						
Clupeidae	*Etrumeus teres*	4.58	8.61	7.45		17.99	209.42	10.96	1.67
	Sardinops sagax	411.13	38.00	28.37		233.38	219.43	26.05	15.29
	Spratelloides robustus	1.10							
	Clupeiformes spp.		5.51				8.51	8.18	
Creedidae	*Creedia haswellii*	18.57	10.10				7.43		
Dinolestidae	*Dinolestes lewini*	4.37						0.65	0.82
Eel leptocephalii	Eel leptocephalii			0.79	1.01				
Engraulidae	*Engraulis australis*		0.55	0.69		5.24	16.34	8.71	11.66
Evermannellidae	*Evermannella* sp.							0.40	
Gadiformes	Gadiformes spp.			0.69					
Gobiesocidae	*Alabes* sp. 1	6.74				0.88	4.17		
	Gobiesocidae sp. 1	1.85	1.25			0.86			
	Gobiesocidae sp. 2						2.73		
Gobiidae	*Afurcogobius suppositus*					7.23	17.55		
	Gobiidae sp. 2					2.62	7.95		
	Gobiidae sp. 3	10.96	2.00	11.98			1.86	4.28	1.94
Gonorhychnidae	*Gonorhynchus greyii*				0.25				
Gonostomatidae	*Cyclothone* spp.		27.68	47.51	19.70		1.21	6.68	3.47
	Gonostomatidae spp.				0.25		0.58		
Idiacanthidae	*Idiacanthus anstrostomus*			0.55	0.25				
Labridae	Labridae sp. 1	48.72	2.75	4.18		14.39	61.93	0.33	3.16
	Labridae sp. 2					2.01			
	Labridae sp. 3								1.63
	Labridae sp. 4						2.12		
	Labridae sp. 5			0.79		0.88	3.98	0.42	
	Labridae sp. 6				0.54				
Leptoscopidae	Leptoscopidae sp. 1	12.13		2.21					
Melamphaeidae	Melamphidae spp.			0.28				0.46	
Monacanthidae	Monacanthidae spp.	22.19	3.86	4.41		6.04	6.65	1.16	
Moridae	Moridae spp.	4.49	3.86	5.90		2.01	2.96		
Mullidae	Mullidae sp. 1			0.63			5.65	9.69	9.56
Myctophidae	*Benthosema suborbitale*		0.92	9.03				0.43	
	Ceratoscopelus warmingii						0.41		
	Centrobranchus sp. 1			0.63	0.31				
	Diaphus "slender" spp.		26.43	14.08	1.01		3.94	169.00	246.25
	Diaphus "stubby" spp.							2.06	
	Diogenichthys atlanticus		7.61	25.11	5.94		0.58	26.27	18.77
	Hygophum spp.		2.63	12.88	7.68		0.41	0.85	
	Lampadena spp.			2.89			3.12	12.72	40.35
	Lampanyctodes sp.				0.62				
	Lampanyctus spp.		30.99	20.32	2.04		1.98	41.17	15.81
	Lobianchia dofleini		0.92	0.79					0.85

Family	Species	Winter				Summer			
		Station B (mean #/m^3)	Station C (mean #/m^3)	Station D (mean #/m^3)	Station E (mean #/m^3)	Station B (mean #/m^3)	Station C (mean #/m^3)	Station D (mean #/m^3)	Station E (mean #/m^3)
	Lobianchia gemellari			5.49					
	Myctophum asperum							13.94	20.17
	Myctophum phengodes		1.48	2.01	0.31		0.54	0.97	
	Notoscopelus resplendens		2.03	6.38	0.76			0.42	2.21
	Notolynchnus valdiviae							0.33	
	Scopelopsis multipunctatus		59.33	54.37	17.26				
	Symbolophorus spp.		4.15	0.69				2.48	
Nemipteridae	*Nemipterus* sp. 1						2.05		
Nomeidae	*Psenes whiteleggii*				0.21				
Notosudidae	Notosudidae sp. 1		1.11	1.37	1.23				
Odacidae	Odacidae sp. 1	25.90				4.89	5.16		
Paralepidiae	Paralepididae spp.			1.66				4.21	6.01
Pempheridae	Pempheridae spp.	1.85				6.46	8.48		
Percicthydae	*Howella* sp. 1				0.25		0.58		
Percophidae	*Enigmapercis reducta*					0.43	5.13		0.58
Phosichthydae	*Vinciguerria* spp.		23.61	26.29	1.88		4.63	52.65	31.31
	Pollichthys sp. 1				0.92				
Pinguipedidae	*Parapercis* spp.	2.54	0.69						
Platycephalidae	Platycephalidae sp. 1					0.43	2.69		
	Platycephalidae sp. 2					2.62			
Plesiopidae	*Paraplesiops* sp. 1		0.69						
Paralychthidae	Paralychthidae sp. 1						0.58		
Pleuronectiformes	Pleuronectiformes spp.	5.04		4.94		2.01	2.44	1.14	0.27
Pomacentridae	*Chromis* sp. 1						0.41	3.05	13.42
	Amphriopion sp. 1		0.55				0.58	0.40	0.27
	Pomacentridae sp. 1						2.12		
	Pomacentridae sp. 2						2.36	0.80	0.55
Scombridae	*Scomber australasicus*						4.60	9.53	4.62
	Scombridae sp. 1	0.62							
Scopelarchidae	*Scopelarchus* sp. 1		7.34	1.11					
Scorpaenidae	Scorpaenidae sp. 1		6.76	6.04	6.50				3.25
	Scorpaenidae sp. 2			1.11			5.69		0.85
	Scorpaenidae sp. 3	0.62				2.62			
	Scorpaenidae sp. 4							2.06	
Serranidae	Serranidae sp. 1		7.70			1.75			
Sillaginidae	*Sillago* spp.			1.11		3.49			
Sternoptychidae	*Argyropelecus* spp.				0.44				
	Sternoptychidae spp.								1.36
Stomiidae	Stomiidae sp. 1		1.38						
Syngnathidae	Syngnathidae sp. 1			1.11		2.62			
	Syngnathidae sp. 2	1.38							
Terapontidae	Terapontidae sp. 1					5.24	4.25		
Trachichthydae	Trachichthydae sp. 1	2.19							
Tripterygiidae	Tripterygiidae sp. 1	2.20	1.38			13.44	2.54	2.33	0.27
Unidentified	Unidentified sp. 1	20.12	9.88	11.70			2.68		

Higher concentrations of larvae were caught in summer bongo net tows than in winter (Mann-Whitney test, p=0.01 (Figure 5.6), although concentrations of larval fish in January 2004 overall were quite low compared to other summer samples, from the two and a half years of sampling across the Two Rocks transect (see Chapter 2). There was no significant difference between mean larval fish concentrations on the shelf in summer and winter (Mann-Whitney test, p=0.57). There were, however,

significantly greater mean larval fish concentrations offshore (stations D and E) in summer than in winter (Mann-Whitney test, p=0.02).

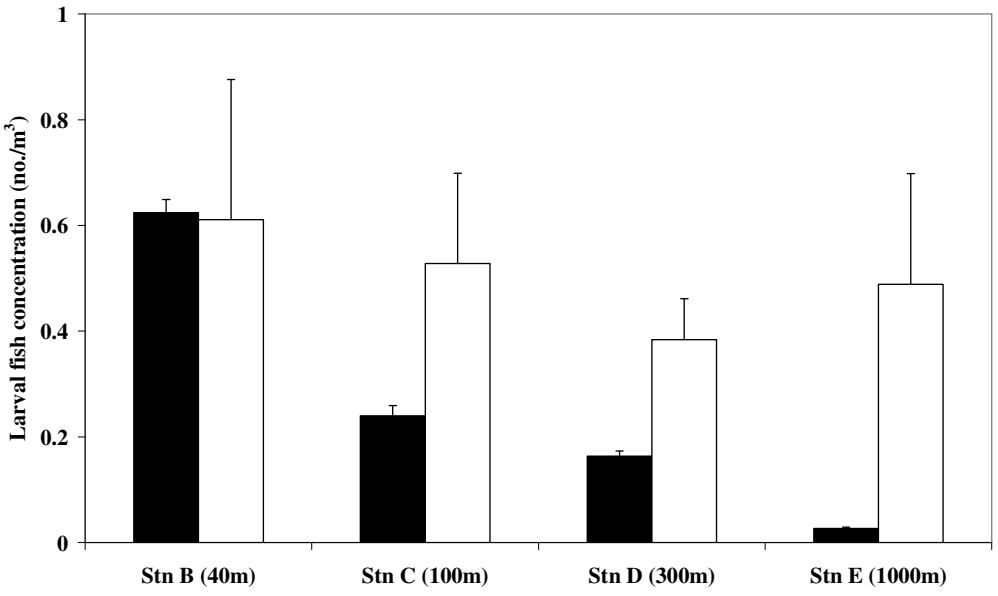

Figure 5.6: Larval fish concentrations from day-time bongo net samples from stations B (40m) to E (1000m), August 2003 and January 2004. Black bars denote winter samples, white bars denote summer samples.

Within seasons, there were greater larval fish concentrations on the shelf than offshore during winter (Mann-Whitney test, p=0.02), but not during summer (Mann-Whitney test, p=0.25).

Comparison of the vertical structure of larval fish concentrations between winter and summer showed that in both seasons across the sampling transect, most fish larvae were found in the upper 70-80m of the water column (Figure 5.7). Larval fish concentrations also tended to be highest in the shallowest depth strata, with the exception of station C in summer. The thermocline was shallower in winter than in summer, however, on both cruises, most larval fish were found above this feature.

During winter, the shelf station assemblages were dominated by *S. sagax*, which comprised 57% of all larvae caught. Larvae of *Cyclothone* spp. (6%) and *Lampanyctus* spp. (6%) were the next most abundant taxa. The winter offshore assemblage was dominated by larvae from the oceanic families Myctophidae, Gonostomatidae, Paralepididae, Sternoptychidae and Phosichthydae, with 85% of larvae caught belonging to these families. *Cyclothone* spp. were the most abundant larvae, with *D. atlanticus* (17%) and *S. multipunctatus* (11%) also common.

As with the winter shelf assemblage, the summer shelf assemblage was dominated by clupeiform larvae, with *S. sagax* (42%) and *E. teres* (20%) the most abundant. *Engraulis australis* larvae were also present in summer, but at much lower concentrations (1%). Larvae from the Carangidae (20%) and Labridae (7%) were also common in summer shelf samples. Similarly to the winter offshore assemblage, the summer offshore group was dominated by oceanic larvae from the Myctophidae, Gonostomatidae, Paralepididae, Sternoptychidae and Phosichthydae, with 87% of larvae in summer offshore samples belonging to these families. Larvae of *Diaphus* "slender" spp. were the most abundant (57%), with larvae of *Vinciguerria* spp. (7%) and *Lampanyctus* spp. (6%) also common.

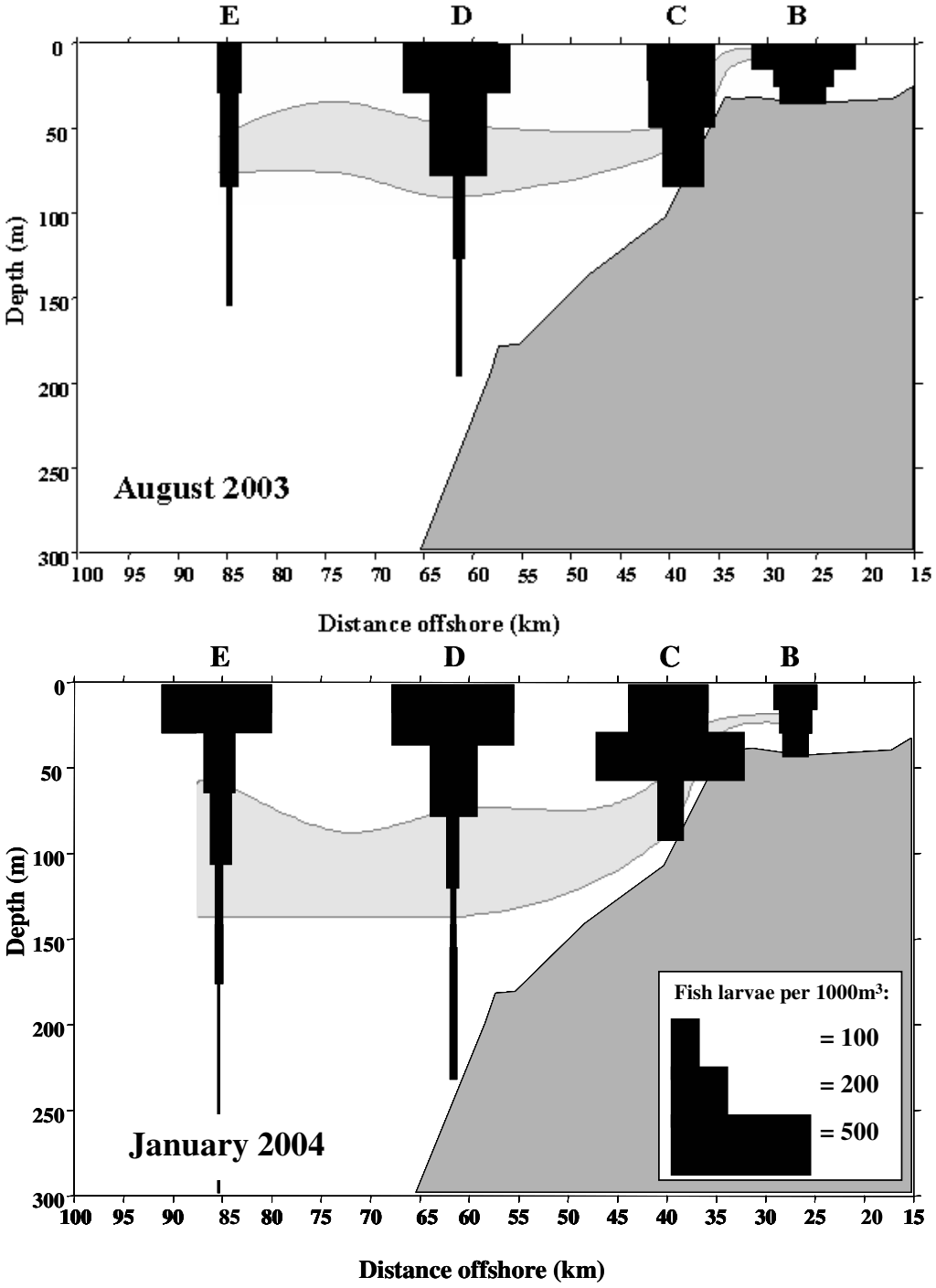

Figure 5.7: Total concentrations of larval fish (number /1000m^3) across the Two Rocks transect from shelf to offshore waters in August 2003 and January 2004 (night EZ data only). Concentrations are plotted at the median depth of each depth stratum, and the approximate upper and lower boundaries of the thermocline are shown by the shaded bands.

5.3.3 Horizontal and vertical structure of larval fish assemblages

Analysis of similarity (ANOSIM) tests between samples taken from EZ nets, with data combined to 150m depth (total larval fish caught between 0-150m depth, divided by total volume sampled 0-150m), and bongo net samples revealed no difference between larval fish assemblages sampled by the two net types, during either season (winter: R=0.06, p=0.20, summer: R=-0.06, p=0.71). There was also no difference between the integrated EZ net data between day and night tows (R=-0.14, p=0.94). The two sample groups were therefore combined to provide greater replication when examining differences in assemblages between seasons, and across the sampling transect within seasons. Using this combined dataset, larval fish assemblages between the winter and summer cruises, from all sampling stations, were significantly distinct (R=0.20, p=0.007). When shelf samples only were examined, there was a significant difference between seasons (R=0.20, p=0.03), however, the distinction between seasons was much stronger when only offshore samples were considered (R=0.75, p=0.002). Within summer cruise samples, shelf larval fish assemblages were strongly distinct from offshore assemblages (R=0.97, p=0.001). This distinction was also present during winter, but was much weaker (R=0.37, p=0.01).

Larval fish assemblages from the shelf in summer were best distinguished from those in winter by greater concentrations of Carangidae spp., and Labridae sp. 1 in summer (Table 5.3). The main distinction between summer and winter offshore assemblages was the dominance of *Diaphus* "slender" spp. in summer, as well as the higher concentrations of *D. atlanticus* in winter. Within each cruise, summer shelf samples were distinguished from summer offshore larval fish assemblages by greater concentrations of *Diaphus* "slender" spp. and *D. atlanticus* offshore, and greater

concentrations of Carangidae spp. on the shelf (Table 5.3). In contrast, there were no distinguishing species found to strongly separate winter shelf and winter offshore assemblages.

Table 5.3 Results of similarity percentage (SIMPER) comparison between larval fish assemblages from bongo net and EZ net data combined, to find taxa which distinguish between shelf and offshore assemblages, during summer and winter.

SIMPER comparison	Distinguishing taxa
Summer shelf vs. winter shelf	Carangidae spp. (More in summer)
	Labridae sp. 1 (More in summer)
Summer offshore vs. winter offshore	*Diaphus* "slender" spp. (More in summer)
	Diogenichthys atlanticus (More in winter)
Summer shelf vs. summer offshore	*Diaphus* "slender" spp. (More offshore)
	Carangidae spp. (More on shelf)
	D. atlanticus (More offshore)
Winter shelf vs. winter offshore	None for which [$\overline{\delta i}$ /SD($\overline{\delta i}$)] <1.4

5.3.4 Horizontal and vertical distributions of abundant species

Larval *S. sagax* were found commonly on both cruises, with higher concentrations on the shelf than offshore (Mann-Whitney test, p=0.01) (Figure 5.8). In winter, *S. sagax* larvae were found only at stations B and C, while in summer, larvae were found farther offshore, at stations D and E as well. A similar pattern was observed for the larvae of another clupeid, *E. teres* (Figure 5.8). *Sardinops sagax* larvae showed a fairly even distribution through the water column on both cruises, although they were found in greater abundance in the upper two depth strata at station B in winter (Figure 5.8). Although conditions on both cruises were not strongly stratified in the upper 100m of the water column, most *S. sagax* larvae were located above the thermocline.

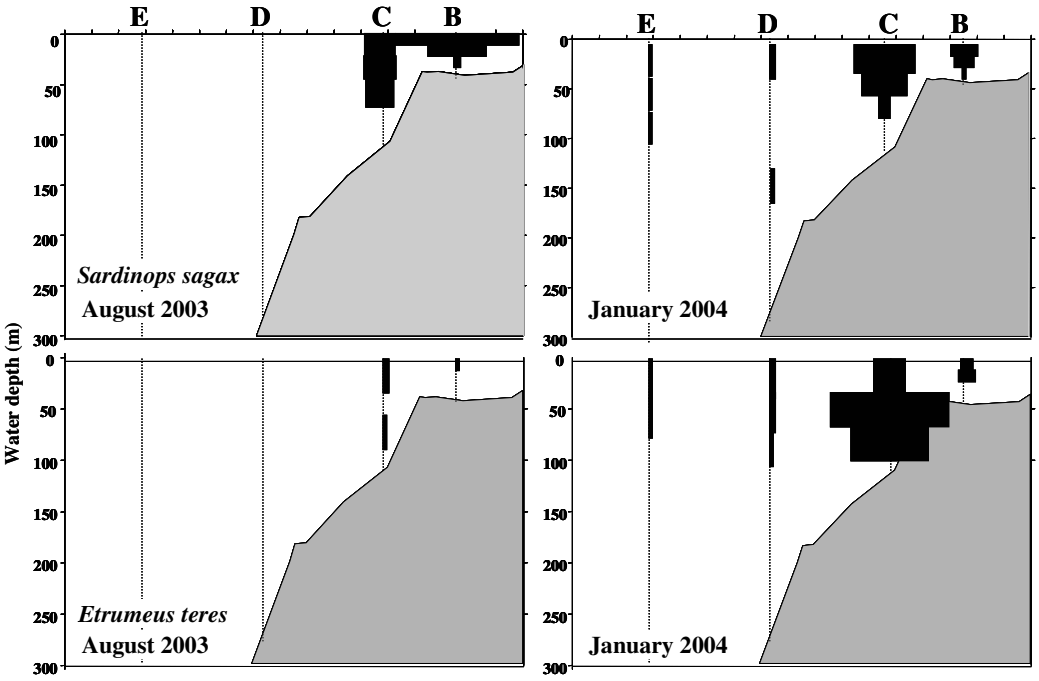

Figure 5.8: Concentrations of A) larval *Sardinops sagax*, and B) *Etrumeus teres* (number /1000m^3) across the sampled transect from shelf to offshore waters, EZ night samples only, August 2003 and January 2004. Concentrations are plotted at the median depth of each depth stratum.

Etrumeus teres showed a similar depth distribution to *S. sagax*, although it was found in higher concentrations in the two deeper strata in summer at station C (Figure 5.8). The highest concentrations, at station C between 30 and 55m depth, corresponded to the base of the mixed layer, where ADCP data had shown the currents to be to the northwest (Figure 5.5).

In contrast, larvae of the most abundant Myctophidae species, *Diaphus* "slender" spp., were found across the outer shelf and offshore regions on both cruises, with higher concentrations offshore than on the shelf (Mann-Whitney test, p=0.03) (Figure 5.9). These larvae were much more abundant in summer (Mann-Whitney test, p=0.02). Larvae of *Vinciguerria* spp. were found across the outer shelf and offshore on both

cruises, however, they were most abundant at stations D and E in summer, and at stations C and D in winter (Figure 5.9. There was no significant difference between mean concentrations of *Vinciguerria* spp. between shelf and offshore stations, reflecting their tendency to be found further inshore than *Diaphus* "slender" spp. (Mann-Whitney test, p=0.70).

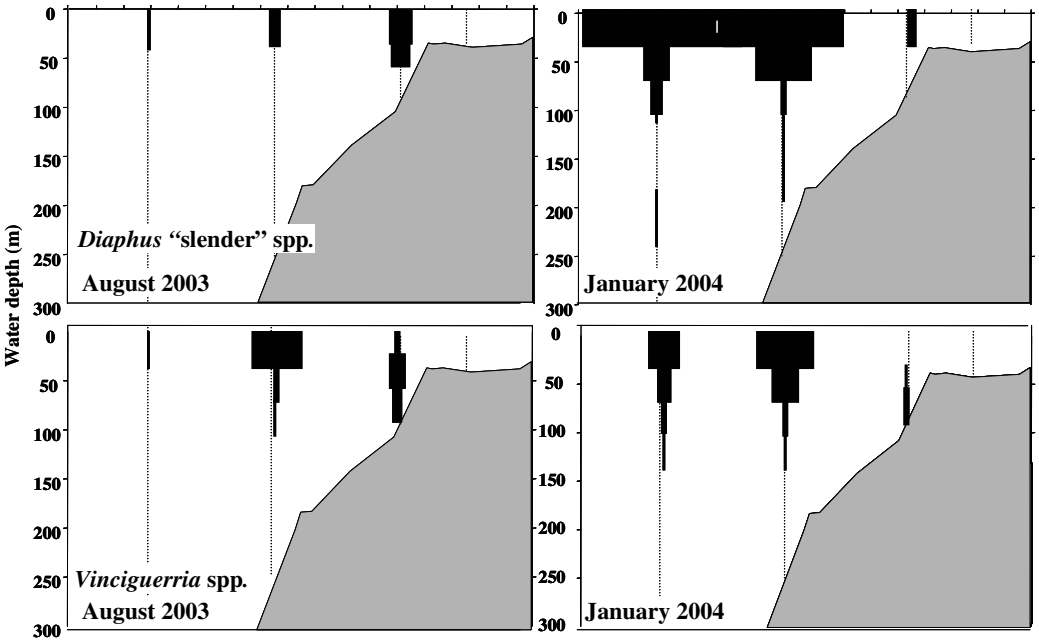

Figure 5.9: Concentrations of A) larval *Diaphus* "slender" spp., and B) *Vinciguerria* spp. (number /1000m^3) across the sampled transect from shelf to offshore waters, EZ night samples only, August 2003 and January 2004. Concentrations are plotted at the median depth of each depth stratum.

Diaphus "slender" spp. were found throughout the water column at the two offshore stations, but were most abundant in the upper 60-70m (Figure 5.9). A broader depth distribution of *Diaphus* "slender" spp. larvae at station D in summer corresponded to a deeper thermocline at this station. Larvae of *Vinciguerria* spp. were similarly

distributed to D*iaphus* "slender" spp., also being more abundant in surface strata (Figure 5.9).

Larvae of some coastal species were also found to have a more offshore distribution in summer, especially those with neustonic larvae, such as Tripterygiidae spp. (Kingsford, 1988; Hickford and Schiel, 2003) (Figure 5.10). In contrast, larvae that tended to avoid the surface layer, such those from the Gobiidae (Leis, 1991; Olivar and Sabates, 1997), had a less obvious offshore distribution in summer than in winter (Figure 5.10). Tripterygiidae larvae were found predominantly in the surface depth strata on both cruises, but were more abundant in summer. In contrast, Gobiidae larvae avoided the surface depth stratum, especially in summer, and were largely positioned at or below the thermocline (Figure 5.10), in areas of weak, south-easterly current flow (Figure 5.5).

Examination of length data indicated that small *S. sagax* larvae tended to be found at station B, with significantly larger larvae found at stations C to E (Figure 5.11) (Mann-Whitney test, $p<0.001$). Larvae at the surface at station D had the greatest mean length, although there were no statistically significant differences between lengths of larvae between stations C, D and E. Larvae of *E. teres* at station B were also significantly smaller than those at stations C to E (Mann-Whitney test, $p=0.03$), but the difference was weaker and less obvious than for *S. sagax* (Figure 5.11).

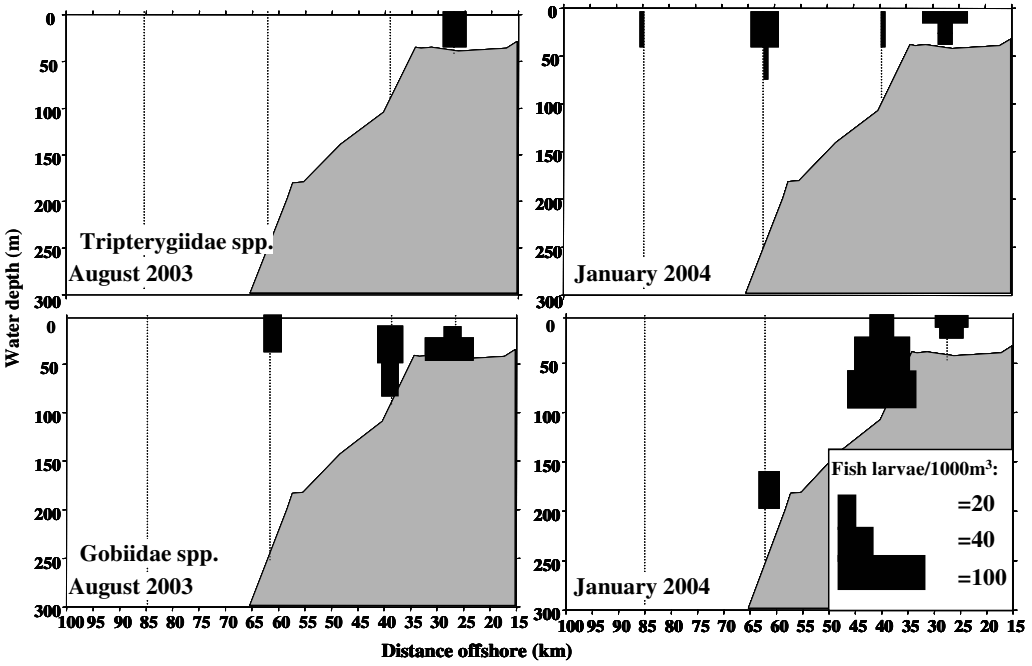

Figure 5.10: Concentrations of A) Tripterygiidae spp., and B) Gobiidae spp. (number /1000m^3) across the sampled transect from shelf to offshore waters, EZ night samples only, August 2003 and January 2004. Concentrations are plotted at the median depth of each depth stratum.

Tripterygiidae larvae did not show a directional increase in size with distance from shore, and no statistically significant difference was present between lengths of larvae from different stations, partly because of the small samples sizes at some stations. However, all larvae caught at stations D and E were large (> 6mm, with a mean length of 8.2mm or more), with smaller larvae only being found at shelf stations (Figure 5.12). Neither *S. sagax*, *E. teres* or Tripterygiidae spp. appeared to show any length-dependent changes in depth preference.

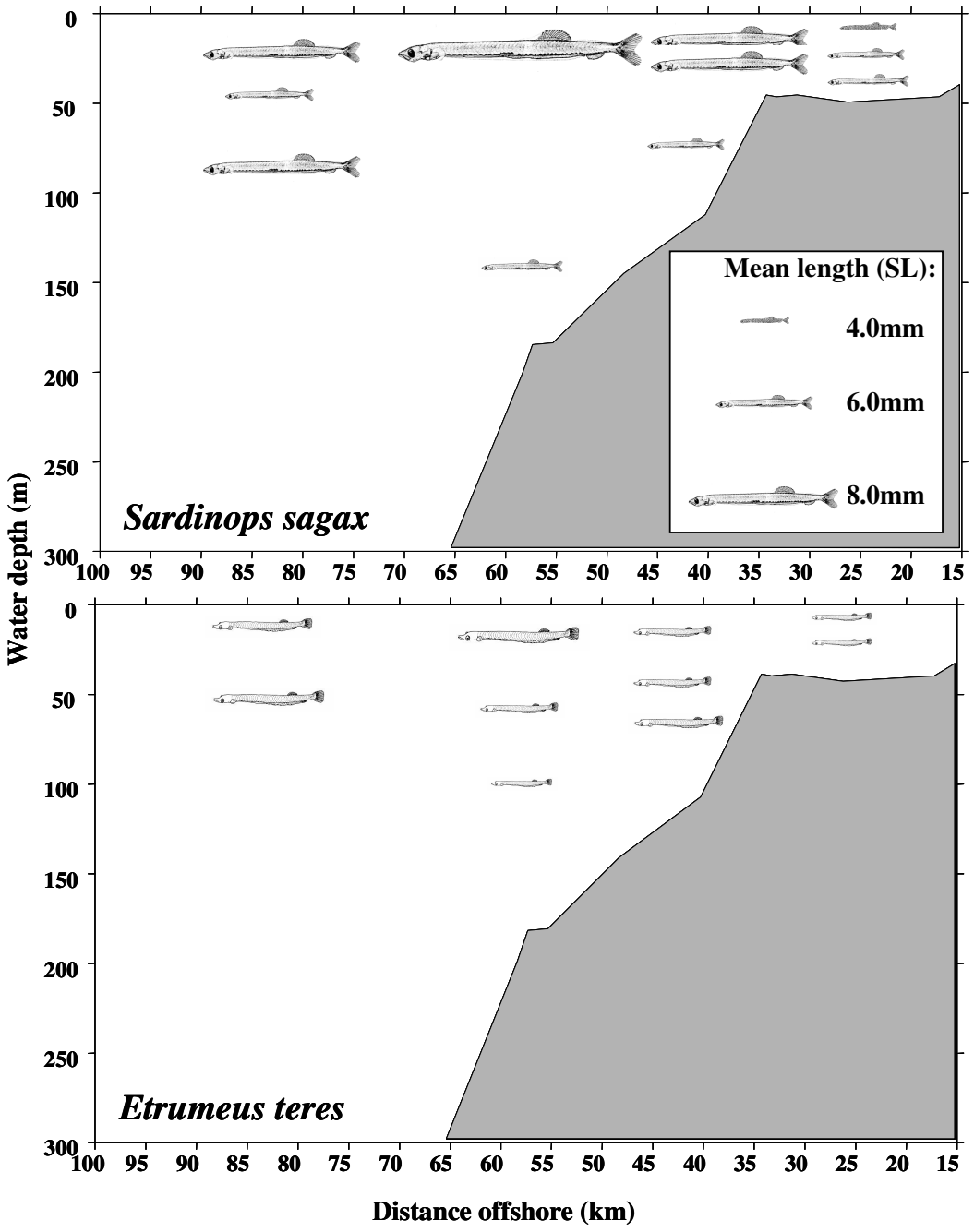

Figure 5.11: Mean length (mm SL) of larval *Sardinops sagax* and *Etrumeus teres,* across the sampled transect from shelf to offshore waters in January 2004. Data from EZ nets only are shown, and lengths are plotted at the median depth of each depth stratum. Graphics: Matarese *et al.,* 1989 and Olivar and Fortuno, 1991.

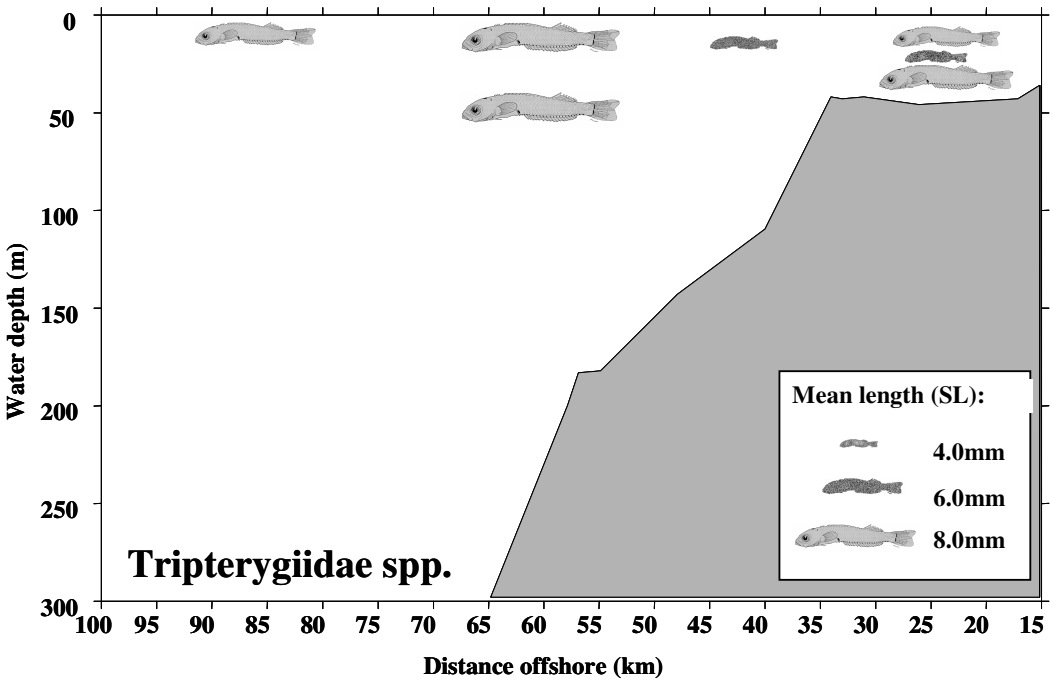

Figure 5.12: Mean length (mm SL) of larval Tripterygiidae spp. across the sampled transect from shelf to offshore waters in January 2004. Data from EZ nets only are shown and lengths are plotted at the median depth of each depth stratum. Graphic: Beltran-Leon and Herrera, 2000.

5.4 Discussion

5.4.1 Larval fish assemblage structure and oceanographic processes

Data presented here highlight some of the differences between the larval fish assemblages off south-western Australia during summer and winter. Patterns in species abundances and distribution were consistent with those known for the area, during summer and winter oceanographic regimes (see Chapter 2). Larvae collected were from fishes which occupy a wide variety of adult habitats. These included coastal and shelf reef species (Gobiidae, Moncanthidae, Pempheridae), sandy bottom and seagrass associated species (Callionymidae), pelagic species (*S. sagax, E. teres, Scomber australasicus*), tropical vagrants (*Chromis* sp. 1) and oceanic species

(*Scopelopsis multipunctatus*, *Vinciguerria* spp. and other Myctophidae larvae) (Neira *et al*., 1998; Hutchins and Swainston, 1986).

Assemblages were found to be largely distinct between seasons, between depth strata, and between shelf and offshore sampling stations. Seasonal differences were likely due to the contrasting oceanographic conditions present during summer and winter, to which adult fish have presumably adapted their spawning times and locations. Winter oceanographic conditions off south-western Australia are characterised by strong southward flow of the warm Leeuwin Current, and the close proximity of this current to the coast (Pearce and Pattiaratchi, 1999) (see Chapter 2). There are fewer tropical vagrants being transported south by the Leeuwin Current in winter, as most tropical reef fish do not appear to spawn in winter on the reefs north of the study area, such as the Abrolhos Islands (Hutchins, 1991; Hutchins and Pearce, 1994). The absence of the Capes Current in winter results in a lack of northwards transport of temperate reef fish larvae, so the influx of larvae of coastal or shelf species from north or south of the study area is limited. Transport processes during this time are predominantly along-shore, largely as a result of the strong flow of the Leeuwin Current. Cross-shelf transport processes are comparatively much weaker, and generally result only from meanders and jets off the Leeuwin Current (Cresswell, 1991; Pearce *et al*., in press). The winter larval fish assemblage on the shelf and slope in this study was therefore composed largely of Clupeidae larvae, which were found shorewards of the main body of the Leeuwin Current, and oceanic fish larvae associated with shoreward intrusions of the Leeuwin Current. The offshore station E was situated beyond the outer boundary of the Leeuwin Current, resulting in a very low concentration, low diversity assemblage of oceanic species. Larval fish assemblages reflected the high

oceanographic connectivity across the shelf and offshore in winter, with assemblages not differentiated as strongly between shelf and offshore samples compared to in summer.

Oceanographic conditions during summer were distinct from those during winter, with the Leeuwin Current weaker, and farther from the shore. Some tropical vagrant larvae were caught within the Leeuwin Current on the outer shelf, and in offshore waters, mostly from the Pomacentridae. Oceanic larvae, such as those from the Myctophidae, were found in high concentrations at stations D and E in summer, especially near the surface. While these stations were located in water of Leeuwin Current origin, the flow of the current would have been much weaker than in winter, as indicated by the ADCP data. Southward transport of larvae in offshore waters during summer is therefore likely to be lower than in winter. A small eddy feature appeared to be situated over stations D and E during the January cruise (A. Pearce, CSIRO, *pers. comm.*, 2005), therefore it is also possible that this feature in some way retained or concentrated these larvae around the area sampled.

Over the inner shelf in summer, the Capes Current was flowing northwards, inshore of the Leeuwin Current, resulting in the influx of slightly cooler, more saline water over the inner shelf, and the transport of some temperate reef fish larvae northwards past the study area. The presence of two opposing currents on the shelf and slope appeared to reduce the spatial connectivity across the shelf, with larval fish assemblages distinct between water masses (see Chapter 2). However, this effect was partially offset by the presence of surface, seaward Ekman transport, caused by the strong southerly winds characteristic of south-west Australia during summer

(Gersbach *et al.*, 1999), which was clearly evident from the ADCP data. Westward currents were present in the mixed layer at all stations sampled in January. This effect resulted in larvae of some coastal and shelf species being more widely distributed across the shelf, and being found farther offshore, in summer than in winter.

Fish larvae with neustonic vertical distributions showed greater offshore distribution during summer, as the westerly component of the current at stations C and D weakened with depth. Larvae of taxa that tended to avoid the surface waters, such as the Gobiidae (Leis, 1991; Gray, 1993), showed more similar horizontal distributions between the two seasons. Surface neuston net samples from the same cruises discussed here also showed that larvae and small juveniles from families such as the Carangidae, Clupeidae, Monacanthidae and Tripterygiidae were distributed much farther offshore in summer than in winter (Chisholm, 2004). This effect of vertical distribution on horizontal transport has also been found previously in other coastal oceans, including off north-west America (Bailey, 1981), and south-eastern Australia (Smith, 2000). Hickford and Schiel (2003) also found the larvae of reef fish off the east coast of New Zealand, including those from the Tripterygiidae, to be dispersed farther from shore than would be expected, given their demersal eggs. These findings contrast with those of Leis and Miller (1976), and Gray (1993), who found Tripterygiidae larvae in highest abundance at inshore sites. Offshore dispersal of reef fish larvae may therefore be more common on exposed coasts (Hickford and Schiel, 2003).

5.4.2 Vertical structure of larval fish assemblages

Depth distribution of larval fishes may be affected by the position and strength of the thermocline (Ahlstrom, 1959, Kendall and Naplin, 1981). The broad depth strata sampled in this study did not allow fine-scale vertical distribution of larval fish to be established. Conditions during both cruises were not strongly stratified, due to a storm before the winter cruise, and strong southerly seabreezes before the summer cruise (Koslow *et al.*, 2005). However, some taxa were still shown to be potentially aligning themselves to physical gradients. Larvae of some taxa, such as *S. sagax*, and *Diaphus* "slender" spp., were mostly found above the thermocline. In addition, *Diaphus* "slender" spp. were found to be distributed deeper in the water column at station D than station E in summer, corresponding to a deeper mixed layer at station D. Tripterygiidae larvae were generally neustonic, but showed a broader depth distribution closer to shore: a pattern also found by Hickford and Schiel (2003). This pattern explains the rather selective offshore distribution of Tripterygiidae larvae, with a wide range of larval sizes found on the shelf, and only larger larvae found offshore. Conversely, Gobiidae larvae were mostly found at or below the thermocline, at depths with little or no offshore current component, and were not shown to be dispersed as far offshore as the more neustonic larvae. The vertical distributions of larvae from different species were therefore seen to be potentially influential in determining their offshore horizontal distributions.

Some studies have suggested that fish larvae may actively position themselves at depths of maximum prey item abundance, or at the chlorophyll maximum layer (Matsuura *et al.*, 1993; Groenkjaer and Wieland, 1997). The chlorophyll-α profiles across the transect were very different between the two seasons studied, with much

higher chlorophyll-α concentrations in winter than in summer, and a shallower chlorophyll maximum layer in winter. There was a slight increase in chlorophyll concentration at station B in January, possibly as a result of the northwards flow of the Capes Current past the transect (Pearce *et al*., in press). Chlorophyll α concentrations were highest in inshore waters during the winter cruise. This may have been a result of the large cold-front system that crossed the study area a few days before the August cruise. The high wave and wind energy, and resultant mixing caused by this frontal system, may have led to the re-suspension of organic matter in coastal and shallow shelf waters, and to the increased chlorophyll concentrations recorded (Mullin *et al*., 1985; Gallucci and Netto, 2004). Larval fish were not found to be aligning themselves to the chlorophyll maximum layer on either cruise. Depth distributions of potential prey items (microzooplankton and mesozooplankton) are not always coincident with the chlorophyll maximum layer, however, data on the depth distributions of potential prey items for larval fish were not available for this study.

5.5 Conclusions

The initial hypothesis, that the distinctive oceanographic conditions found between summer and winter would be reflected in the larval fish assemblages, was supported. The distribution of species across the shelf and offshore appeared to be strongly influenced by the current regime at the time of sampling. The vertical depth preferences of larvae also influenced their horizontal position, especially with regard to surface-dwelling fish larvae.

Chapter 6: Larval fish assemblage structure in two mesoscale Leeuwin Current eddies, eastern Indian Ocean

6.1 Introduction

Mesoscale eddies are commonly formed in association with major current systems, such as in the Kuroshio Current region (Kimura *et al*., 2000), in the California Bight (Logerwell *et al*., 2001), the Agulhas Current (Lutjeharms *et al*., 2003; Quartly and Srokosz, 2004), the Eastern Australian Current (Nilsson and Cresswell, 1981), and in the southeastern Indian Ocean (Cresswell and Griffin, 2004). As they propagate seawards, they influence spatial patterns of both physicochemical water properties (Brandt, 1981; Fang and Morrow, 2003; Morrow *et al.,* 2003) and the distribution and structure of biological populations (Brandt, 1981; Batten and Crawford, 2005; Govoni, 2005).

The biological structure within a mesoscale eddy is a product of both the initial entrainment of planktonic organisms from the source waters of the eddy, and of the evolution of these communities over time (Griffiths and Wadley, 1986; Lobel and Robinson, 1988; Mackas *et al*., 2005; Miller *et al*., 2005). Physical processes within eddies influence biological characteristics, with cyclonic eddies characterized by the upwelling of cooler water from depths, and subsequent nutrient and phytoplankton enrichment, and anti-cyclonic eddies characterized by the reverse situation (McGillicuddy and Robinson, 1997; Kimura *et al.*, 2000; Kasai *et al.*, 2002). In addition, eddies may undergo convective, and other mixing processes in isolation from the surrounding ocean (Tranter *et al*., 1980). Biological communities within mesoscale eddies may originate from different locations from those in surrounding waters, and be subject to a different range of physical gradients.

Several authors (e.g. Nakata *et al.,* 2000; Logerwell *et al.,* 2001; Logerwell and Smith, 2001; Nishimoto and Washburn, 2002) have emphasized the potential influence of eddies on fish eggs and larvae. Eddies may concentrate and retain larvae in a particular area (Kasai *et al.,* 2002; Okazaki *et al.,* 2002), or act as a means of offshore entrainment and dispersion (Heath, 1992). They may also modify the biological environment with regards to both larval prey and predators. The ichthyoplankton assemblage in an eddy will be influenced by both the effects of the eddy on larval transport and advection, and the effects of food availability, and larval predator concentration, within the eddy.

This study describes the ichthyoplankton assemblages collected from two mesoscale eddies associated with the Leeuwin Current, sampled approximately 300-600km off the coast of south-western Australia. Larval fish assemblages were compared both between the two eddies, and also between the different horizontal and vertical zones of each eddy. Environmental factors correlated with larval fish assemblages within the eddies were investigated.

6.2 Material and methods

6.2.1 Sampling

A 23 day cruise aboard the *RV Southern Surveyor* was undertaken in October 2003 to investigate the dynamics of two eddies (one cold-core, cyclonic and one warm-core, anti-cyclonic) located more than 500km off the south-western Australian coast (Figure 6.1, Figure 6.2).

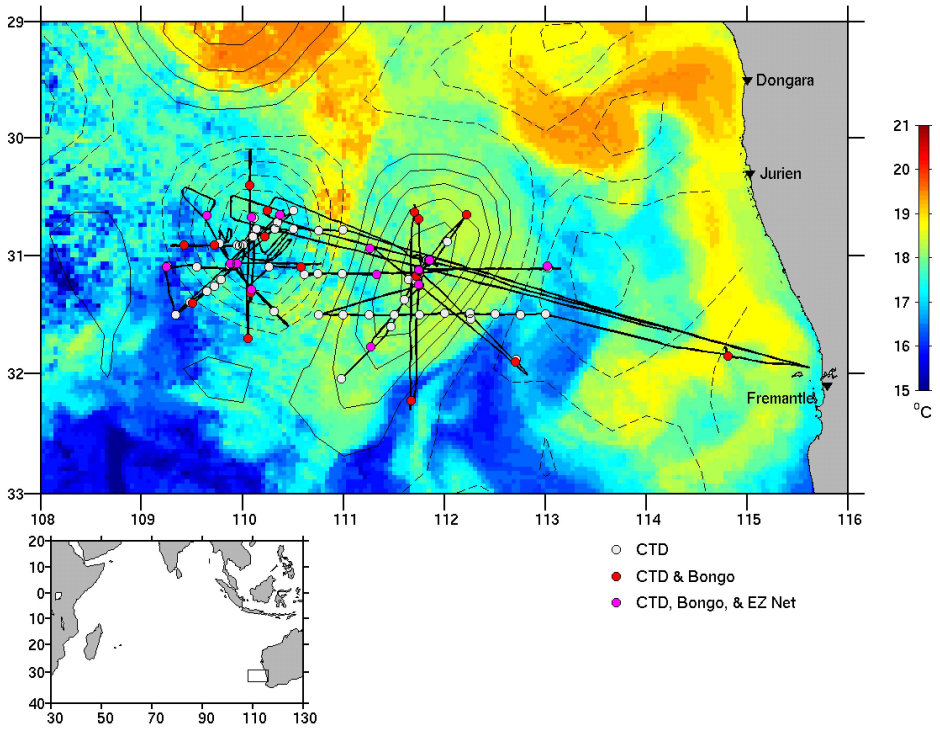

Figure 6.1: Warm and cold-core eddies sampled in the eastern Indian Ocean, October 2003. Sea surface temperature (colour) and sea surface height (contours) are shown, with ship track and sampling stations overlayed. Note the warm inter-eddy jet entrained between the eddies from the north, and the northwards intrusion of cool subtropical front water east of the warm-core eddy (Waite *et al.*, submitted b).

Multiple CTD, zooplankton and primary productivity samples were taken from three pre-determined zones within each eddy (the centre, body and perimeter). The eddy centre was defined by the zone of zero current flow, the eddy perimeter as the outer edge of what was considered eddy water, and the eddy body was located between these two extremes (Waite *et al.*, submitted b). CTD casts were completed at 97 stations, providing temperature, salinity and fluorescence data to 500m depth.

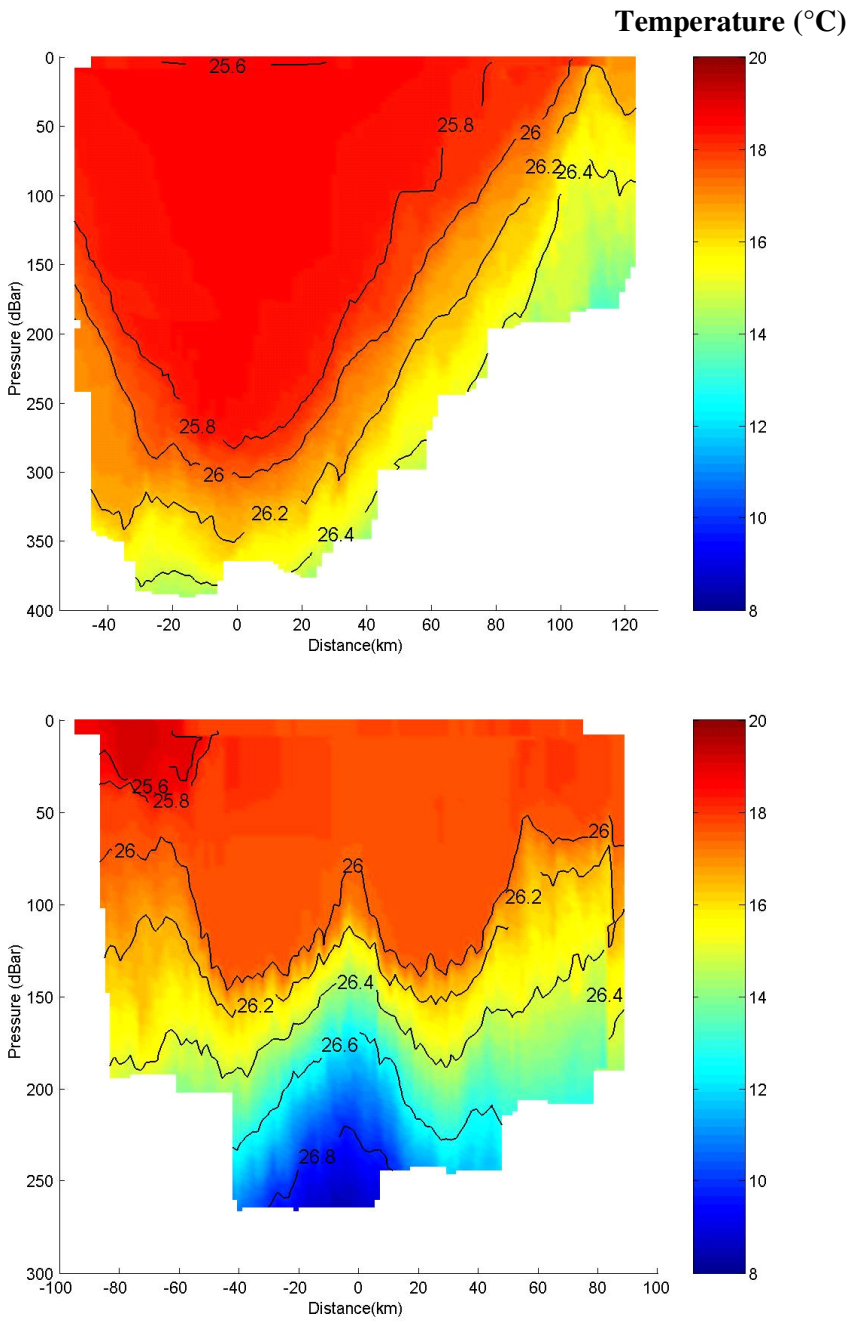

Figure 6.2: Temperature sections of the warm-core eddy (top) and the cold-core eddy (bottom) from Seasoar temperature data. Sigma-t contours are also shown. Note the deep mixed layer at the centre of the warm-core eddy, and the cap of warm water at the surface of the cold-core eddy (Waite *et al*., submitted b).

Fluorescence was strongly correlated with chlorophyll α biomass, and was therefore used as a proxy for chlorophyll biomass (Feng *et al.*, submitted). Seasoar casts (see Waite *et al.*, submitted b) were used to provide continuous temperature sections for each eddy (Figure 6.2).

Plankton sampling was completed using both opening and closing EZ nets and bongo nets. EZ nets were fitted with 335μm mesh (mouth area 1.0m^2), and were towed at 2 knots from 450m depth. EZ net tows were completed in the centre, body and perimeter of each eddy, once during the day, and once at night (12 tows total), with total towing time ranging from 30 to 46 minutes per station. These tows were used to compare between eddies, and between depth strata within each eddy. Five depth strata were sampled, and were chosen to correspond to depths sampled along the Two Rocks transect (see Chapter 5). They covered the approximate depth of the mixed layer (0-30m), the chlorophyll maximum layer (30-80m), and below the chlorophyll maximum layer (80-150m). Two additional strata were selected for the eddies cruise: one to the bottom of the mixed layer in the warm-core eddy (150-300m), and one sampling below the eddy (300-450m). A flowmeter fitted on the net allowed the calculation of volumes sampled per stratum (mean 478m^3±33 SE).

Bongo nets were fitted with 100 and 355μm mesh (mouth area 0.196m^2), and were towed obliquely from 150m depth. Thirty six bongo net tows were carried out in total: 17 in the warm-core eddy, and 19 in the cold-core eddy. Volumes sampled by the bongo net averaged 324m^3 (±25 SE), with total tow times from 14 to 22 minutes. Nets were towed at a speed of about 2 knots, with sampling undertaken during both day and night.

Plankton samples were fixed in 10% buffered formaldehyde immediately after collection. Larval fish were removed from the 355µm bongo net samples, and from all EZ net samples with the aid of a dissecting microscope. They were preserved in 70% ethanol, and identified to family, and species where possible, using the relevant available literature relating to oceanic species (Moser and Ahlstrom, 1974; Moser *et al.,* 1984; Olivar *et al*., 1999; Moser and Watson, 2005). Larvae of some taxa could not be resolved to species level, including some species of *Lampanyctus, Hygophum* and *Diaphus*. These larvae were either assigned a type name if they were sufficiently distinctive, e.g. *Hygophum* species "B", *Diaphus* "slender" spp. (*sensu* Moser and Ahlstrom, 1974), or referred to as a possible combination of two species, e.g. *Lampanyctus australis/alatus*. The description and distribution of *Hygophum* species are not well determined in the study area, and *Hygophum* species "B" was considered to belong to the *Hygophum macrochir* complex *sensu* Hulley (1981).

6.2.2 Data Analyses

Larval fish abundances per cubic metre of seawater sampled were determined, with mean concentrations and standard errors calculated for replicate tows. The juvenile and adult stages (defined *sensu* Leis and Carson-Ewart, (2000)) of small mesopelagic fishes, such as the Myctophidae and Phosichthydae, were commonly caught in night samples. These fish were excluded from larval fish assemblage analyses, as they were not true larvae, but for completeness, abundances of juvenile and adult Myctophid species are given in Appendix 5.

Assemblage structure was investigated with the Primer-6 software package (Clarke and Warwick, 2001). EZ net larval fish assemblage data were used to compare assemblages between different depth strata within each eddy, with the six (3 day and 3 night) samples taken within each eddy for each depth stratum acting as replicates for the whole eddy. Bongo net samples were used for the remaining assemblage analyses. To reduce the weighting of dominant species, concentrations from both net types were ($\log_{x+1}$) transformed prior to assemblage analyses (Clarke and Warwick, 2001). Bray-Curtis similarities between samples were used to construct a triangular similarity matrix, which was then classified to create an hierarchical, agglomerative dendrogram. The significance of the cluster groups created was tested by similarity profile analysis (SIMPROF) (see Chapter 2). Permutation testing was used to determine whether the structure within cluster groups was statistically different from a random result, and at which point the further splitting of cluster groups of samples became spurious (Clarke and Warwick, 2001). Non-metric multi-dimensional scaling (MDS) was also used to provide a 2-dimensional visual representation of assemblage structure.

Analysis of similarity (ANOSIM) (Clarke and Warwick, 2005) was used to test for the presence of significant differences between the larval fish assemblages of the two eddies, using bongo net data (see Chapter 2). The ANOSIM process was also used to determine whether assemblages differed significantly between vertical (EZ net) and horizontal (bongo net) zones within the eddies. Where the analysis of similarity had identified a significant difference in larval fish assemblages between two groups of samples, the similarity percentage routine SIMPER (Clarke and Warwick, 2005) was used to identify the species characteristic of different assemblages, and also those

species for distinguishing assemblages (see Chapter 2). The same ratio was used to identify species useful for discriminating between assemblage groups, with the mean contribution of any one species to the overall dissimilarity between sample groups considered in the same way.

Lastly, the BVSTEP subroutine (Clarke and Warwick, 2005) related larval fish assemblages to four selected environmental variables: sea surface temperature, depth of the mixed layer (as defined with a $0.125\sigma_\theta$ increment from 10m depth (Feng *et al.,* submitted)), the proportional distance from the eddy centre (Feng *et al*., submitted) and areal chlorophyll α biomass (mg/m^2) (Waite *et al.,* submitted b) (see Chapter 3 for more information about the BVSTEP procedure). These environmental variables were chosen as examples of easily measurable, and available, physical, biological and spatial parameters that may reasonably be expected to influence the structure of larval fish assemblages (e.g., Loeb, 1980; Röpke, 1993; Sassa *et al.,* 2004b). The variable, or combination of variables, that best explained the variation in larval fish assemblages was identified.

6.3 Results

6.3.1 Oceanographic conditions

The eddies were originally formed near the south-western Australian coast during May 2003, from a meander structure of the Leeuwin Current (Feng *et al*., submitted). They were fully detached from the current by August/September, and were identifiable as an eddy dipole when sampled in October 2003 (Figure 6.1). The apparent radius (radius where the azimuthal velocity peaks) of the warm-core eddy was 72 km near the sea surface, while the apparent radius of the cold-core eddy was

about 44 km near the sea surface. The peak azimuthal velocity of the warm-core eddy decreased from 75cm/s at 19m depth to around 46cm/s at 250m depth. The peak current in the cold-core eddy was almost constant with depth, at around 60cm/s (Feng *et al.,* submitted).

When sampled *in situ*, both eddies proved to be deep-structured, influencing water column properties to at least 350 - 400m depth. The warm-core eddy showed a typical anti-cyclonic, downwelling structure, with a warm mixed layer penetrating to 250m at the eddy centre, reducing to 100m at the eddy perimeter (Figure 6.2). The warm-core eddy had a stronger vertical shear, and a more diffuse thermocline than the cyclonic cold-core eddy, which was capped with warm, Indian Ocean water. The cold-core eddy therefore had a shallower mixed layer depth, at a minimum of 100m at the eddy centre, and a maximum of about 140m at 20-40km from the eddy centre (Figure 6.2) (Feng *et al.,* submitted). The resultant strong stratification at 100-150m depth in the cold-core eddy, and a lack of current shear below the mixed layer, indicated low turbulent mixing, therefore upwelling generated by this eddy did not strongly influence the mixed layer (Feng *et al.*, submitted). Consequently, the cold-core eddy did not contain high concentrations of chlorophyll biomass: chlorophyll in this eddy was in fact slightly lower than surrounding waters (Waite *et al.,* submitted b). In contrast, the warm-core eddy centre contained higher chlorophyll biomass than surrounding waters, decreasing towards the eddy perimeter, mostly due to a population of large coastal diatoms in the warm-core eddy (Waite *et al.,* submitted b).

While water properties within the mixed layers of the two eddies were largely stable during the cruise, the eddy dipole itself was not an isolated structure, and was shown

to interact with surrounding features. East of the warm-core eddy, there was a sharp temperature front due to intrusion of low-temperature Subtropical Front water from the south (Figure 6.1), while between the two eddies, high temperature tropical Leeuwin Current water was entrained in a jet from the north. Temperature-salinity data suggested that the mixed layer water in the core of the warm-core eddy was mainly composed of Leeuwin Current water, while in the core of the CC eddy, the mixed layer water was similar to the surrounding open ocean water (Sub-tropical Surface Water) (Feng *et al*., submitted).

6.3.2 Vertical structure in larval fish concentrations

Broad patterns in larval fish concentration with depth between the two eddies were initially explored using data from the depth-stratified EZ net tows (Figure 6.3). Temperature and fluorescence profiles show the distinctive structure of the warm-core eddy centre, which was largely uniform for both parameters from the surface to 150m depth. The cold-core eddy showed less variation in the vertical structure of temperature and fluorescence with depth across the eddy, with a deep, subsurface fluorescence maximum at about 60m in the three eddy zones.

In both eddies, larval fish concentrations were very low in the deepest stratum (300-450m), and the majority of larvae appeared in the upper 150m. The warm-core eddy centre had a deep larval fish maximum during the day (80-150m), and few larvae present during the night. The cold-core eddy showed less variation in larval fish concentration, with few differences between eddy zones. In both eddies, larval fish concentrations were very low in the deepest stratum (300-450m), and the majority of larvae appeared in the upper 150m.

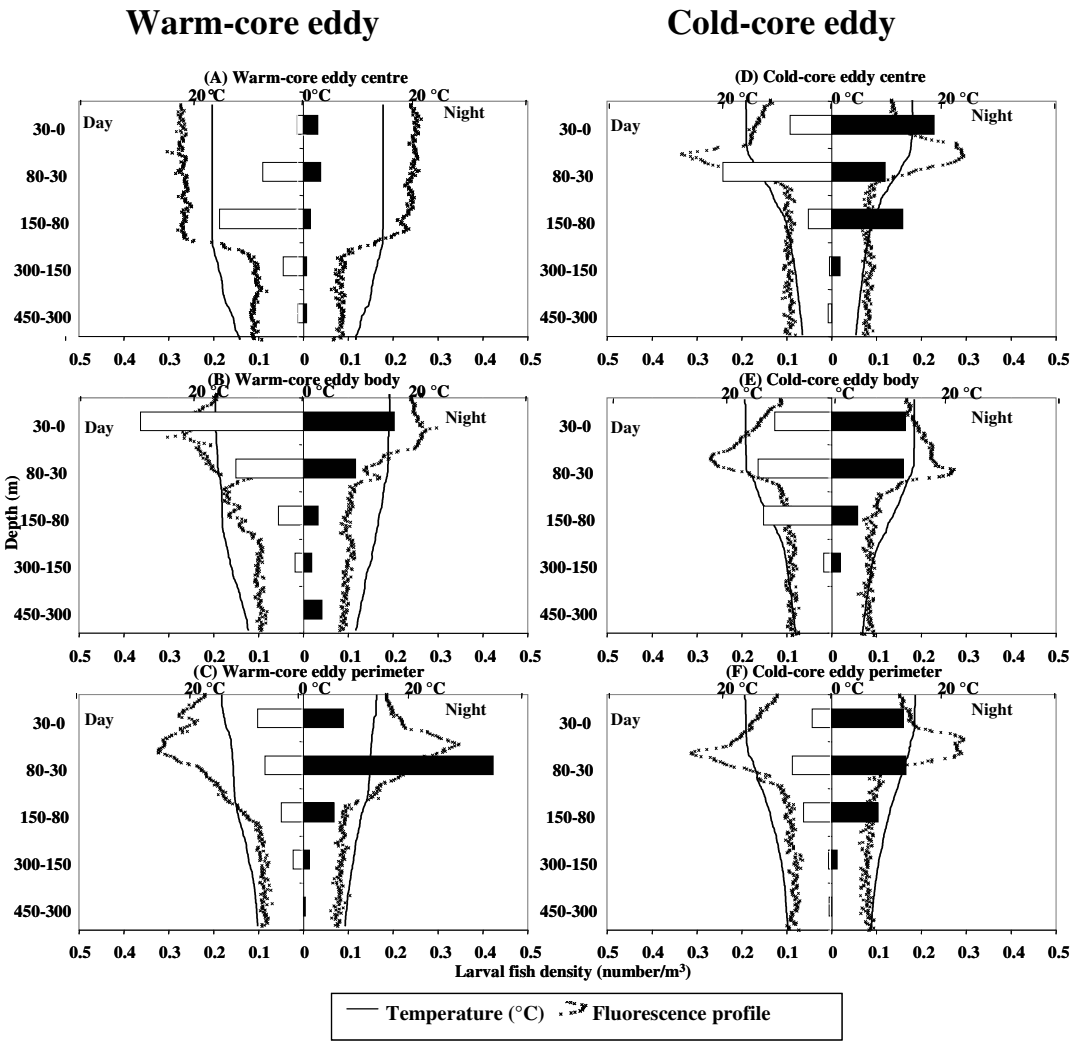

Figure 6.3: (A-F) Vertical distribution of fish larvae in the warm-core (A-C) and cold-core (D-F) eddies, for day and night samples. Concentrations expressed as larvae/m^3 of seawater. Temperature (°C) and fluorescence profiles are also shown.

When concentrations were integrated over the total depth range, there was no significant difference between larval fish concentrations between eddies either during the day (Mann-Whitney test, p=0.89), or at night (Mann-Whitney test, p=0.67). Larval fish from different families showed different depth distributions. Larvae from the

Myctophidae and Phosichthydae had shallower depth distributions than larvae from the Sternoptychidae and Scopelarchidae. Pairwise ANOSIM analyses of larval fish assemblages from all sampled depth strata showed that assemblages in the cold-core eddy were more closely aligned with depth than in the warm-core eddy (Table 6.1).

Table 6.1: Results of ANOSIM pairwise comparison of larval fish assemblages from EZ net data, between different depth strata in the warm-core and cold-core eddies. Test statistics (R) are shown, with statistical significance of result in parentheses. * denotes result significant at <5%, ** denotes result significant at <1%.

(A) Warm-core eddy

Depth strata	450-300m	300-150m	150-80m	80-30m	30-0m
450-300m	X	X	X	X	X
300-150m	R=-0.01 (NS)	X	X	X	X
150-80m	R=0.53 (p=0.02*)	R=0.05 (NS)	X	X	X
80-30m	R=0.67 (p=0.01*)	R=0.36 (p=0.006**)	R=0.03 (NS)	X	X
30-0m	R=0.41 (p=0.02*)	R=0.14 (NS)	R=0.14 (NS)	R=0.11 (NS)	X

(B) Cold-core eddy

Depth strata	450-300m	300-150m	150-80m	80-30m	30-0m
450-300m	X	X	X	X	X
300-150m	R=0.25 (NS)	X	X	X	X
150-80m	R=0.82 (p=0.01*)	R=0.79 (p=0.002**)	X	X	X
80-30m	R=0.81 (p=0.01*)	R=0.91 (p=0.002**)	R=0.21 (NS)	X	X
30-0m	R=0.67 (p=0.01*)	R=0.86 (p=0.002**)	R=0.85 (p=0.002**)	R=0.32 (p=0.03*)	X

The warm-core eddy showed significant differences between assemblages from the shallowest three depth strata, and the deepest (450-300m), but little other distinction, apart from a fairly weak difference between assemblages from 300-150m and 80-30m (R=0.36). Conversely, the cold-core eddy showed significant differences between larval fish assemblages from all depth strata, except for 450-300m vs. 300-150m (R=0.25), and 150-80m vs. 80-30m (R=0.21), and the differences between strata were generally stronger, as shown by higher R statistics.

6.3.3 Depth-integrated bongo net samples

The mean concentration of larval fish for each zone of each eddy was compared between day and night samples using replicated bongo net data (Figure 6.4).

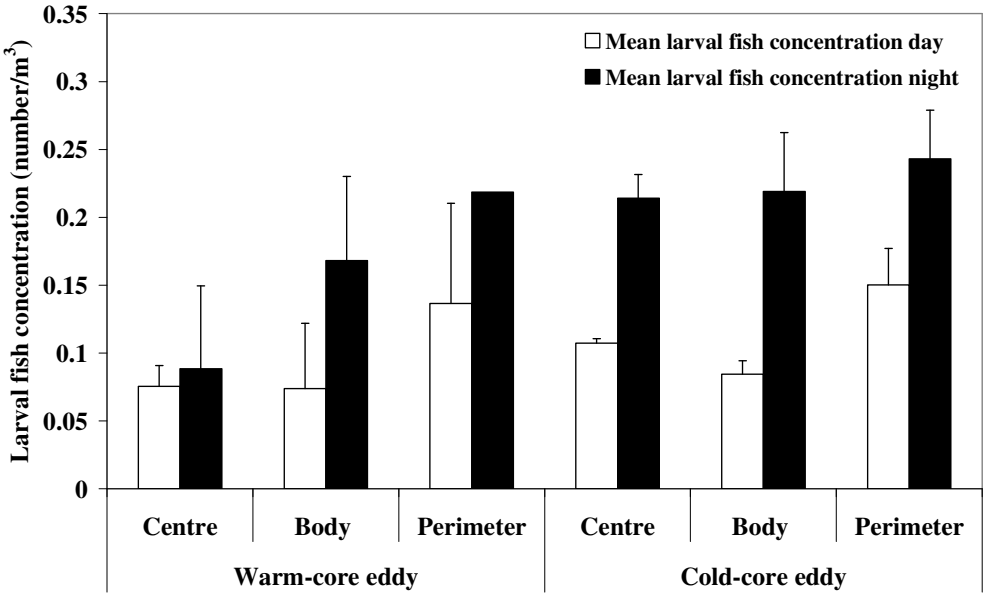

Figure 6.4: Mean concentration (number/m^3) of larval fish in the centre, body and perimeter of the warm-core, and cold-core eddies, calculated from bongo net samples. White columns denote day samples, black columns denote night samples.

Mean larval concentrations ranged from 0.07 larval fish/m^3 in the centre of the warm-core eddy during the day, to 0.24 larval fish/m^3 at the cold-core eddy perimeter at the night. Larval fish concentrations within bongo nets were shown to be significantly higher in the cold-core eddy than in the warm-core eddy (Mann-Whitney test, p=0.04). Concentrations were significantly higher at night in the cold-core eddy than during the day (Mann-Whitney test, p=0.001), but not in the warm-core eddy (Mann-Whitney test, p=0.48). There was no significant difference in mean larval fish concentrations between different zones within either the warm-core eddy (Mann-Whitney test, p=0.17), or the cold-core eddy (Mann-Whitney test, p=0.53).

In both eddies, the vast majority of larvae were from the oceanic families Myctophidae (lanternfish), Phosichthydae (lightfish) and Gonostomatidae (bristlemouths) (Figure 6.5), with six Labridae (wrasse) larvae caught at stations around the eddy perimeters representing the only coastal fish larvae found (see Appendix 4).

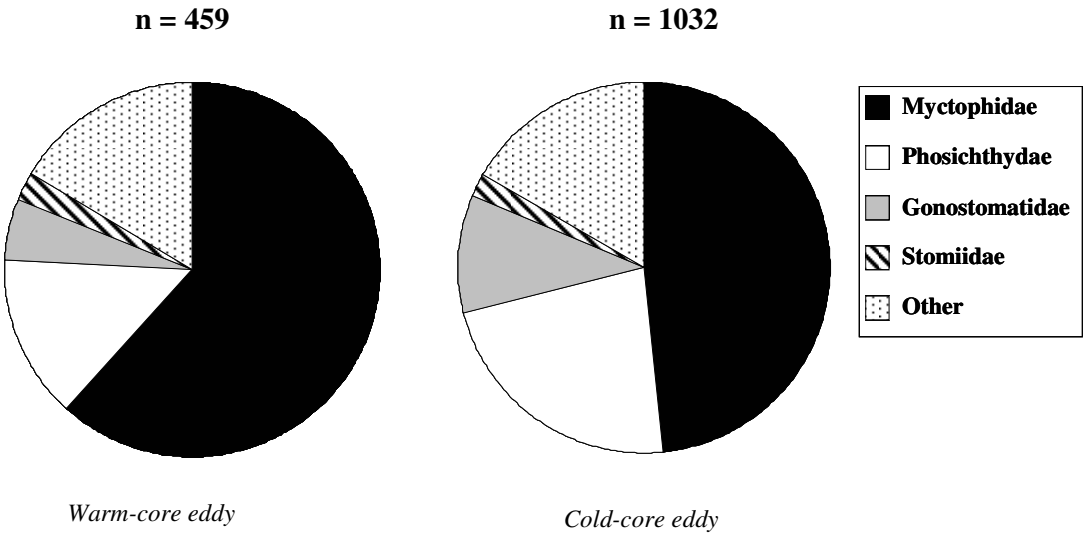

Figure 6.5: Percentage contribution of families to larval fish assemblages in the warm-core and cold-core eddies: Bongo net samples.

The warm-core eddy contained a greater proportion of Myctophidae larvae (62%) than the cold-core eddy (49%) (Mann-Whitney test, p=0.01), and a smaller proportion of larvae from the Phosichthydae (14% versus 23%) (Mann-Whitney test, p=0.002). The warm-core eddy also contained a lower proportion of Gonostomatidae larvae than the cold-core eddy, at 5% and 10%, respectively (Mann-Whitney test, p=0.002). Mean taxon diversity was lower in the warm-core eddy centre than at the perimeter (Mann-Whitney test, p=0.01); no such distinctions existed across the cold-core eddy.

A species list of larval fishes found in the two eddies is given in Appendix 4. In the warm-core eddy, the most abundant species found in the eddy centre was *Diogenichthys atlanticus*, which contributed 69% of the total centre assemblage. This species also contributed 30% of the eddy body assemblage, along with *Vinciguerria* spp. (27%), and *Lampanyctus australis/alatus* (Myctophidae) (15%). At the warm-core eddy perimeter, the assemblage tended to be more diverse, with *Vinciguerria* spp. (21%), *D. atlanticus* (14%), *Lampanyctus australis/alatus* (14%) and *Cyclothone* spp. (Gonostomatidae) (10%) being the most abundant. In the cold-core eddy, *D. atlanticus* and *Vinciguerria* spp. were also common in the eddy centre and body, with *D. atlanticus* contributing 36% and 29%, respectively, and *Vinciguerria* spp. contributing 30% and 29%, respectively. *Vinciguerria* spp. were also common at the cold-core eddy perimeter (21%), with *D. atlanticus* and *Ceratoscopelus warmingii* contributing 20% and 9%, respectively.

A comparison of larval fish assemblages between the warm-core and cold-core eddies was performed using ANOSIM. There was a significant difference between the

assemblages of the two eddies during the day (R = 0.18), and during the night (R = 0.35). The same analysis was then performed within each eddy: between the three eddy zones (centre, body and perimeter), and between the day and night samples from each eddy (Table 6.2).

Table 6.2: Results of ANOSIM analysis to test for differences in larval fish assemblages between eddy zones, and between day and night bongo net samples in the warm-core and cold-core eddies. Test statistic (R) is shown, with statistical significance of result in parentheses. * denotes result significant at <5%, ** denotes result significant at <1%.

Eddy	Centre vs Body	Centre vs Perimeter	Body vs Perimeter	Day vs Night
Warm-core eddy	R=0.59 (p=0.02*)	R=0.50 (p=0.01*)	R=0.04 (NS)	R=-0.11 (NS)
Cold-core eddy	R=0.17 (NS)	R=0.12 (NS)	R=0.11 (NS)	R=0.25 (p=0.02*)

The warm-core eddy assemblages were significantly different between the eddy centre and body (R=0.59), and between the eddy centre and perimeter (R=0.50). The cold-core eddy showed no significant difference between assemblages from any of the eddy zones. Conversely, the cold-core eddy day assemblages were significantly different from those found at night (R=0.25), while there was no difference between day and night assemblages in the warm-core eddy. Similarity percentage (SIMPER) analysis indicated that the differences between zones within the warm-core eddy were largely due to the eddy centre assemblage containing lower concentrations of *Vinciguerria* spp. larvae than either the body or perimeter, and lower concentrations of *L. australis/alatus* than the eddy perimeter.

Seven distinct larval fish assemblage groups were identified across both eddies, using SIMPROF (Figure 6.6).

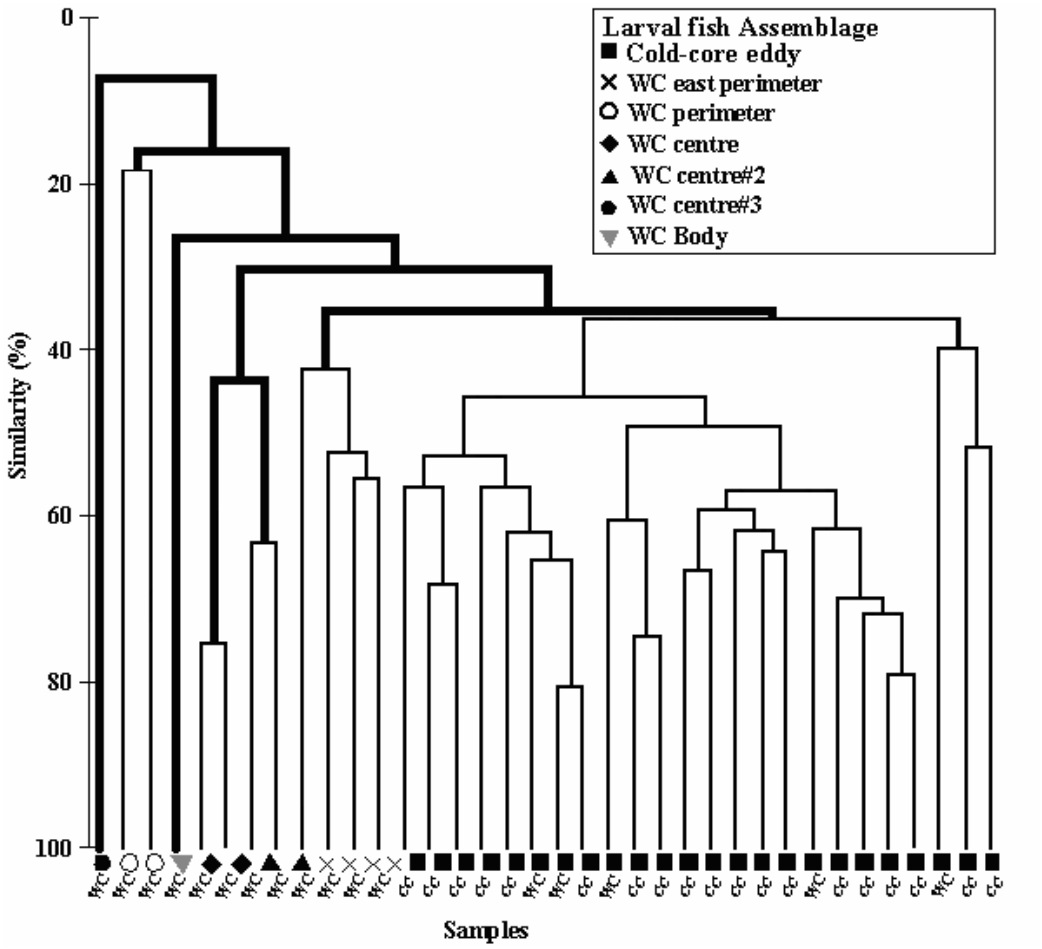

Figure 6.6: Cluster analysis showing larval fish assemblages from all bongo net samples. Similarity profile (SIMPROF) analysis split the samples into seven distinct assemblage groups, and bold lines denote a significant split between assemblages.

The assemblages were named for where their constituent stations were found, as follows: "*cold-core eddy"* assemblage, "*WC east perimeter"* assemblage, "*WC perimeter"* assemblage, "*WC centre"* assemblage, "*WC centre#2"* assemblage, "*WC centre#3"* assemblage and "*WC body"* assemblage. All samples from the cold-core eddy contained one assemblage (*cold-core eddy* assemblage), while all seven

assemblages were identified within the warm-core eddy. Two of these assemblages, the *WC centre night*, and *WC body* assemblages, only represented one bongo net sample each.

Species responsible for splitting samples into these particular assemblages were identified using SIMPER (Table 6.3).

Table 6.3: Comparison of five larval fish assemblages from warm-core and cold-core eddies, identified using SIMPROF analysis: discriminating species identified using SIMPER.

Larval fish assemblages compared	Species responsible for splitting assemblages
Cold-core eddy vs *WC east perimeter*	*L. dofleini* (more in *WC east perimeter*), *L. pussilus* (more in WC *east perimeter*)
Cold-core eddy vs *WC perimeter*	*Vinciguerria* spp. (more in *Cold-core eddy*)
Cold-core eddy vs *WC centre*	*Vinciguerria* spp. (more in *Cold-core eddy*)
Cold-core eddy vs *WC centre#2*	*Vinciguerria* spp. (more in *Cold-core eddy*)
WC east perimeter vs *WC perimeter*	*L. dofleini* (more in *WC east perimeter*), *Vinciguerria* spp. (more in *WC east perimeter*)
WC east perimeter vs *WC centre*	*L. dofleini* (more in *WC east perimeter*), *Vinciguerria* spp. (more in *WC east perimeter*)
WC east perimeter vs *WC centre#2*	*L. dofleini* (more in *WC east perimeter*), *Vinciguerria* spp. (more in *WC east perimeter*)
WC perimeter vs *WC centre*	*D. atlanticus* (more in *WC centre*), *C. sloani* (more in *WC centre*).
WC Perimeter vs *WC centre#2*	*D. atlanticus* (more in *WC centre#2*)
WC centre vs *WC centre#2*	*Cyclothone* spp. (more in *WC centre*), *C. sloani* (more in *WC centre*)

The two assemblages containing only one sample each were omitted from the analysis. The remaining five assemblages were clearly distinguished by variations in

the dominance of a few common species. The *cold-core eddy* assemblage was characterised by higher concentrations of *Vinciguerria* spp. larvae than the other assemblages. The *WC east perimeter* assemblage also contained high concentrations of *Vinciguerria* spp. larvae, but was further distinguished by the presence of *Lobianchia dofleini* (Myctophidae). The *WC perimeter* assemblage was characterised by lower concentrations of *D. atlanticus* than either of the WC centre assemblages. The *WC centre* and *WC centre#2* assemblages were distinguished by the higher concentrations of *Cyclothone* spp. and *C. sloani* in the former.

6.3.4 Variation within and between samples from EZ and bongo nets

The time- and labour-intensive sampling methods used to sample larval fishes in the eddies resulted in less replication of samples than was ideal for rigorous statistical analyses. To examine the potential for spatial and temporal variation within the samples, larval fish assemblages within the top three depth strata (i.e., 0-150m) of the EZ net tows were combined, and compared to the assemblages present within the bongo net tows, using MDS (Figure 6.7). Integrated samples from the upper 150m of the EZ net tows compared well to bongo nets tows, a conclusion reinforced by the non-significant result returned from an ANOSIM comparison between the different net types, across eddy groups (R=0.005). The distance between samples was not perfectly preserved in two dimensions (as evident by the 2D stress of 0.19), but the ordination may still be considered a useful representation (Clarke and Warwick, 2001). Samples collected using both net types from the cold-core eddy were shown to be less variable than those from the warm-core eddy by the closer clustering of the cold-core eddy samples in the MDS plot. The high concentration, high diversity assemblages from the warm-core east perimeter are located at the bottom left of the

plot, with low concentration, low diversity assemblages from the warm-core centre towards the right.

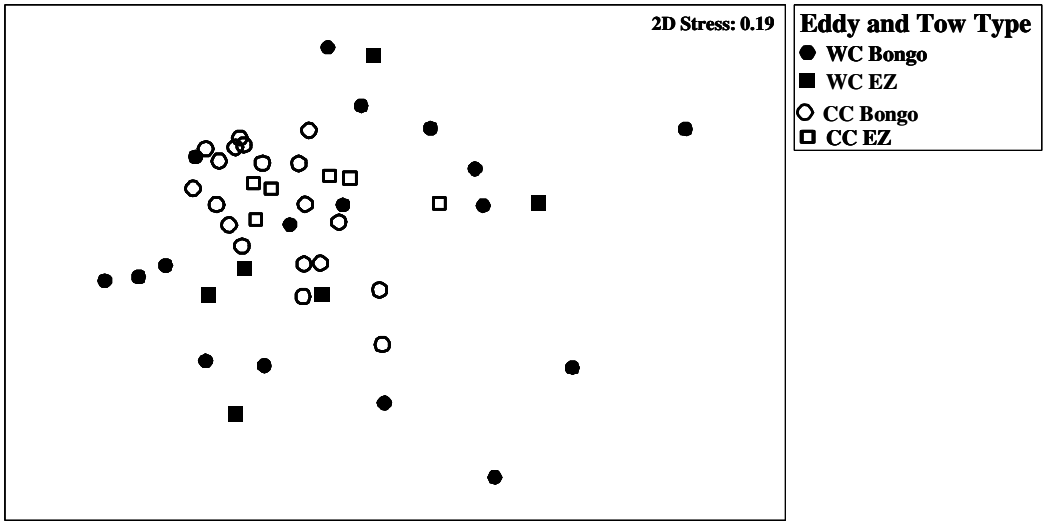

Figure 6.7: Multi-dimensional scaling representation of larval fish assemblages from all bongo net and EZ net (integrated 0-150m depth) samples, in the warm-core and cold-core eddies.

6.3.5 Relation of larval fish assemblages to environmental variables

The correlation of larval fish assemblages, from the bongo net data, with sea surface temperature (SST), depth of the mixed layer (MLD), the proportionate distance from the eddy centre and total areal chlorophyll α biomass (mg/m^2), was analysed using BVSTEP. Assemblages with only one constituent sample (*WC centre night*, and *WC body* assemblages) were excluded from the analysis. BVSTEP was first run on all bongo net data from both eddies, and then within each eddy separately (Table 6.4).

Table 6.4: Correlation of larval fish assemblages in the warm-core and cold-core eddies with environmental variables using the BVSTEP routine. Test statistic ρ is shown for each variable separately, and for the best combination of variables. * denotes result significant at <0.05, ** denotes result significant at <0.01.

Correlations with each variable.	**Both eddies**	**Warm-core eddy**	**Cold-core eddy**
1) Chlorophyll α/m^2	ρ=0.08	ρ=0.05	ρ=-0.07
2) Sea surface temperature	ρ=0.35	ρ=0.29	ρ=0.09
3) Distance from eddy centre	ρ=0.24	ρ=0.30	ρ=0.05
4) Mixed layer depth	ρ=0.18	ρ=0.34	ρ=0.15
Best combination of one or more variables:	2,3,4 ρ=0.40 p=0.002**	1,3,4 ρ=0.37 p=0.03*	None significant at p<0.05

The best combination of environmental variables found to explain the larval fish assemblages across both eddies was SST, distance from eddy centre, and MLD (ρ=0.40), with SST showing the strongest correlation (ρ=0.35). When each eddy was examined separately, larval fish assemblages in the warm-core eddy were best correlated with chlorophyll α biomass, distance from eddy centre, and MLD (ρ=0.37), with MLD best correlated to assemblages (ρ=0.34). There was no significant correlation between any combination of the environmental variables, and larval fish assemblages in the cold-core eddy (ρ=0.15).

6.4 Discussion

This study represents an attempt to quantify the differences in the concentrations, distributions and assemblages of fish larvae between an upwelling and a downwelling eddy, in an oceanic region where larval fish assemblages are poorly known. Concentrations of larval fishes in bongo net samples in the eddies were comparable with concentrations of oceanic fish larvae reported by Sabates (2004) from the oligotrophic Mediterranean, but lower than those found by Olivar and Shelton (1993), and Olivar and Beckley (1994), off the east and west coasts of southern Africa.

The majority of larval fish found were from the oceanic families Myctophidae and Phosichthydae. The Myctophidae is a diverse group of oceanic fishes (>230spp.) with a large global biomass, and their larvae represent a high proportion of the total larvae collected in oceanic plankton samples in any region of the world (Olivar and Beckley, 1994, and references therein). The Phosichthydae is a less diverse group, with 18 species in the family, but the larvae of *Vinciguerria* spp., in particular, are ubiquitous in oceanic regions (Ahlstrom, 1969).

Concentrations of larval fish caught in plankton nets tend to be greater at night, due to decreased net avoidance by the larvae, especially larger larvae which can avoid the nets during the day (e.g. Loeb, 1980). However, larval concentrations did not increase significantly at night in the warm-core eddy, especially in the eddy centre and body. There was no significant difference between day and night assemblages in the warm-core eddy, in contrast to the cold-core eddy. Larval fish concentrations were also more variable in the warm-core eddy, suggesting patchiness in their horizontal distribution within each eddy zone. While many mesopelagic larvae undergo diel vertical

migration (DVM), the range of their migration tends to be contained within the 150m depth stratum sampled by the bongo nets (Loeb, 1980; Röpke, 1993; Sassa *et al*., 2004b). Analysis of the vertical distribution of larval fish within each zone of the two eddies revealed that, similarly to previous studies (Loeb, 1980, Sassa *et al*., 2004b), larval fish concentrations below 150m were generally low, although more larvae were found below 150m in the warm-core eddy than in the cold-core eddy. DVM is therefore not likely to have contributed to the different concentrations and assemblages found in the cold-core eddy between night and day samples.

Considering the contrasting oceanography within the two eddies, it would be expected that there would be correspondingly distinct assemblages between the two eddies, and between the zones within each eddy, as larval fish assemblages have been found to reflect oceanographic and biological conditions (e.g., Olivar and Beckley, 1994; Hare *et al.,* 2001; Okazaki *et al.,* 2002). Analysis between zones in the warm-core eddy showed significant differences in larval fish assemblages between the eddy centre, and the eddy body and perimeter, respectively. These differences were shown to be well aligned to gradients of mixed layer depth and areal chlorophyll α biomass, reflecting the distinct assemblages found between the eddy centre, with a deep mixed layer, and the eddy perimeter, with a shallower mixed layer, and higher chlorophyll biomass (Waite *et al*., submitted b). No such distinctions existed across the cold-core eddy, where all samples taken were considered to contribute to the same assemblage. This result may reflect the high connectivity that the upper 150m of the cold-core eddy had with the surrounding ocean, as compared to the warm-core eddy.

The main factor structuring larval fish species assemblages at different depths was the depth preferences of different taxonomic groups. Larvae from families such as the Myctophidae and Phosichthydae were found at shallower depths than those from the Sternoptychidae and Scopelarchidae, as found in other regions (e.g. Loeb, 1980; Röpke, 1993; Sassa *et al*., 2004b). Larval fish assemblages in the cold-core eddy were strongly separated with depth, especially above and below the thermocline at 80-150m depth, caused by the warm sub-tropical Indian Ocean "cap" water overlying colder, upwelled deep water. In contrast, the warm-core eddy was well mixed to 300m depth in the eddy centre, with a much shallower mixed layer depth at the eddy perimeter (Feng *et al*., submitted). Vertical distributions of mesopelagic fish larvae are affected by light, temperature, mixed layer depth and prey concentrations (Loeb, 1980; Heath, 1992; Röpke, 1993; Sassa *et al*., 2004b), and many of these parameters varied significantly with depth in different zones of the warm-core eddy. This probably resulted in the weak relationship observed between larval fish assemblages and depth in the warm-core eddy.

The structure of the cold-core eddy was distinct from that of the warm-core eddy, but it was not a "typical" upwelling, cold-core eddy, of the type which usually results in enhanced primary production (e.g. Kimura *et al.,* 2000; Mizobata *et al.,* 2002). Chlorophyll biomass was shown to be greater in the warm-core eddy than in the cold-core eddy: an unexpected result if the rotation of the eddies was considered to be the only potential source of nutrient enrichment and subsequent primary productivity (Waite *et al*., submitted b). However, other anti-cyclonic eddies off the east and west coasts of Australia have been shown to support substantial chlorophyll biomass, through mechanisms such as offshore entrainment of productive shelf waters (Griffin

et al., 2001), and prolonged surface water cooling in winter, followed by deep convective mixing (Tranter *et al.*, 1980). Griffin *et al*. (2001) also showed that cyclonic eddies off south-west Australia were not associated with significant surface chlorophyll. The traditional concept of productive cyclonic eddies and oligotrophic anti-cyclonic eddies may therefore not be completely valid for the study region, which has implications for regional estimates of productivity, and for elucidating influences on recruitment to fisheries (Waite *et al*., submitted b).

While the warm-core eddy centre was considered to contain Leeuwin Current water (Feng *et al*., submitted), any neritic fish larvae entrained at eddy formation (April-May 2003) would have metamorphosed or died by the time of sampling (October 2003). Given the low connectivity of this eddy with the surrounding ocean, the re-population of the eddy centre with oceanic fish larvae would be a slow process. Stable isotope analysis suggested that larval fish were preferentially targeting food sources derived from large phytoplankton carbon, such as that found in the large diatoms of the warm-core eddy (Waite *et al.,* submitted a). It is therefore unlikely that the assemblage within the warm-core eddy centre was food limited, and that the low concentrations and diversity of fish larvae within the eddy centre were a result of limited penetration of species from surrounding waters, as found by Griffiths and Wadley (1986), in other temperate Australian warm-core eddies.

The warm-core eddy eastern perimeter contained a distinctive larval fish assemblage. These samples were taken within an intrusion of low-temperature, high fluorescence Subtropical Front water, which was entrained northwards along the eastern perimeter of the warm-core eddy before and during the cruise period (Feng *et al*., submitted).

The presence in this study zone of the larvae of typically cold water fish species, such as *L. dofleini* and *L. pusillus* (Nafpaktitus, 1978; Paxton *et al.,* 1989) suggested the influence of Subtropical Front water at the warm-core eddy eastern perimeter. This was reflected in the alignment of larval fish assemblages to gradients of sea surface temperature across the two eddies, indicating both a distinction between assemblages from the two eddies, as well as the separation of assemblages from the cold Subtropical Front water. The remaining larval fish assemblages were distinguished by variations in the dominance of species such as *D. atlanticus,* and *Vinciguerria* spp., which are commonly found across temperate and tropical habitats (Nafpaktitus, 1978; Paxton *et al.,* 1989). This suggests that their varying concentrations with respect to the warm-core eddy feature (especially the eddy centre) were a result of the differing response of larvae of these species to physical and biological gradients (e.g., Loeb, 1980; Nishimoto and Washburn, 2002; Heath, 1992; Röpke, 1993; Sassa *et al.,* 2004b).

6.5 Conclusions

The warm-core eddy contained larval fish assemblages distinct from those in the cold-core eddy, and lower larval fish concentrations overall, especially in the eddy centre. Most of the observed differences between assemblages related to differences in the relative contributions of common species. Distinctions in larval fish assemblages across the warm-core eddy were probably due to both its isolation from the surrounding ocean, as well as the northwards entrainment of Subtropical Front water around the eastern perimeter of the eddy. Larval fish assemblages were more variable within the warm-core eddy, both across eddy zones and within depth strata, than across the cold-core eddy. Larval fish assemblages within both eddies were largely

composed of oceanic species. It was not possible to ascertain the influence of the eddies in entraining coastal fish larvae off the shelf, as larval duration among fish species is typically less than the age of the eddies when sampled (4-5months). However, although the eddies were old, they still contained a population of coastal diatoms, highlighting their potential role in offshore advection of coastal fish larvae. This topic will be the subject of future work off south-western Australia.

Chapter 7: Conclusions and recommendations

7.1 Larval fish assemblages

The larval fishes collected during the course of this study were largely those of temperate, Indo-Pacific and oceanic fish species. Larvae of coastal species, especially those with benthic eggs, were common in inshore waters, while larvae of pelagic and reef-associated species were abundant on the continental shelf. Clupeiform larvae were particularly dominant in shelf samples, although their abundance was highly variable between seasons, and between years. Larvae of *Engraulis australis* and *Spratelloides robustus* showed clear seasonal and spatial distribution patterns, while larvae of *Sardinops sagax* and *Etrumeus teres* were found throughout the year, with high interannual variability in abundance. Oceanic species, from the Myctophidae, Phosichthydae and Gonostomatidae, dominated offshore assemblages. The influence of the Leeuwin Current was evident during autumn, with the presence of tropical fish larvae at stations sampled within the Current (e.g., *Chromis* sp. 1).

Larval fish concentrations were comparable with those found off other oligotrophic coasts, such as off eastern Australia (Smith and Suthers, 1999), and in the Agulhas Current off South Africa (Beckley and Ballegooyen, 1992), and slightly higher than those found off north-west Australia (Sampey *et al*., 2004). They were lower than larval fish concentrations found off the more productive coasts of southwest Africa (Olivar and Shelton, 1993), Peru (Vélez *et al.,* 2005), and California (Loeb *et al.*, 1983).

Larval fish assemblages off south-western Australia showed strong temporal and spatial structure, and were closely correlated to water masses. Inshore larval fish assemblages were the most predictably seasonal, with shelf assemblages more variable within seasons, and offshore assemblages showing the weakest seasonality. Larval fish species distributions were linked to adult spawning times and locations, and the influence of cross-shelf and along-shore oceanographic processes. This concurs with the findings of Smith and Suthers (1999), for south-eastern Australia, Cowen *et al.* (1993), in the Atlantic, and Hare *et al.*, (2001), off north-eastern America, and confirms the over-riding influence of water mass location and strength on larval fish distributions in oceanographically dynamic regions.

Oceanographic processes were shown to be highly seasonal within the study region, with larval fish distributions and assemblages correspondingly different between summer and winter oceanographic conditions. The association between larval fish assemblages and water masses between summer and winter oceanographic regimes is represented schematically in Figure 7.1.

An inshore larval fish assemblage (distinct between summer and winter) was present in shallow coastal waters. In winter, spatial connectivity across the shelf was high, due to the strength and location of the Leeuwin Current across shelf and offshore stations. Larval fish assemblages reflected this, and were not strongly distinct from station B (40m depth) out to station E (1000m depth). Southward transport as a result of the strong Leeuwin Current during winter was high, and indicated poor larval fish retention. This was demonstrated by the low concentrations of *S. sagax* larvae on the shelf during June and July, despite high GSI data from the Fremantle sardine fishery,

indicating high adult spawning activity. When station E was located offshore of the Leeuwin Current, in STSW, a distinct larval fish assemblage was found.

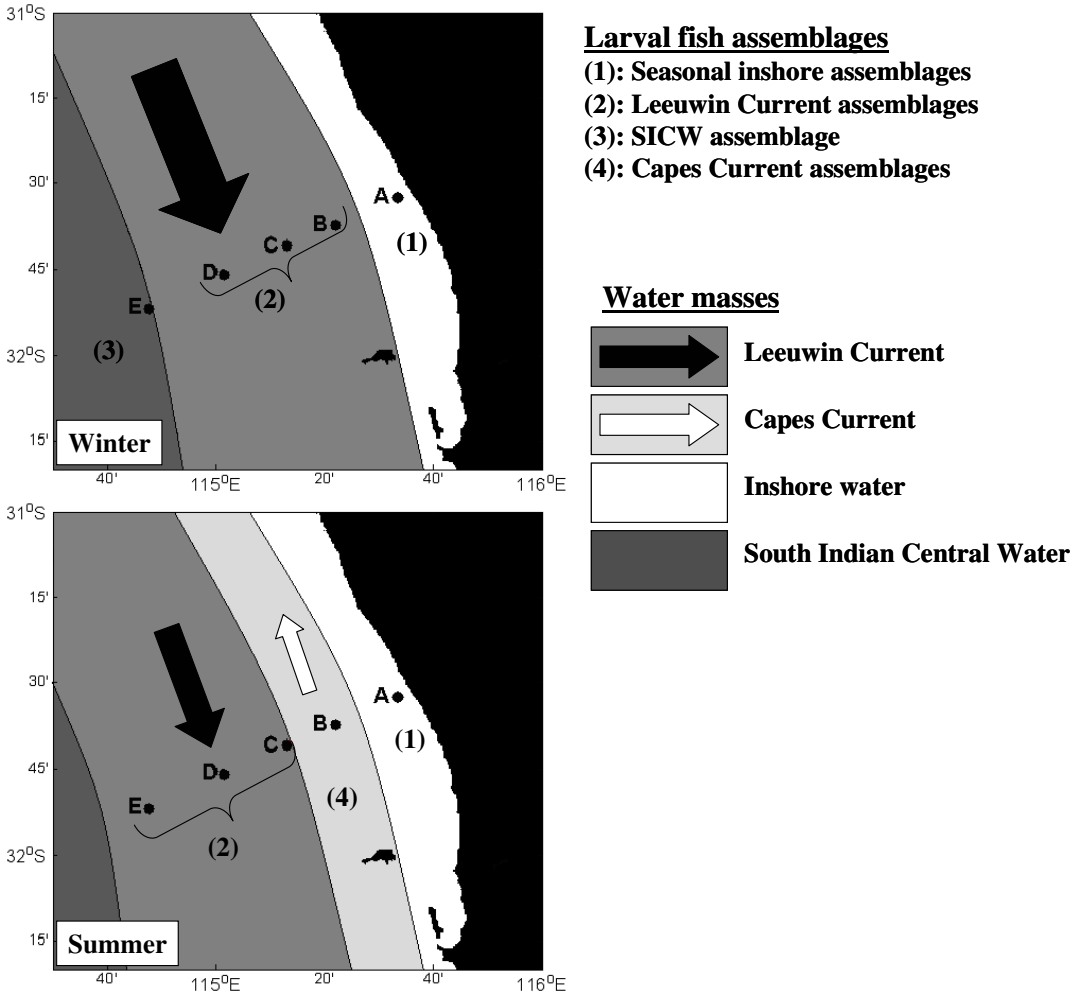

Figure 7.1: Schematic representation of larval fish assemblage structure in winter and summer oceanographic regimes off south-western Australia. Transect stations, larval fish assemblages, and water masses are shown.

In summer, both alongshore transport and spatial connectivity across the shelf were weaker. Larval fish assemblages reflected these conditions, with assemblages from the inner shelf in summer, i.e., within the Capes Current, distinct from those on the

outer shelf, in the Leeuwin Current. However, larvae with shallow or neustonic distributions showed the potential for offshore transport during summer. ADCP data confirmed the presence of offshore Ekman transport in the upper water column during summer, as a result of strong southerly wind stress. This offshore transport existed across the shelf, and across water mass boundaries. Thus, the vertical position of larvae in the water column was also influential on their cross-shelf distribution, with species showing deeper depth preferences retained closer to shore. *Sardinops sagax, Etrumeus teres*, and a species of Tripterygiidae, in particular, showed evidence of offshore larval dispersal.

Meanders and eddies have the potential to change the relative positions of larval fish assemblages, due to their effects on cross-shelf transport. In this study, mesoscale Leeuwin Current eddies were found to influence larval fish assemblages even when well offshore (~500km). While larval fish assemblages in old (about 5 months), offshore eddies were largely oceanic, assemblages in an anti-cyclonic eddy (warm-core) and a cyclonic eddy (cold-core) were distinct from each other. However, the effects of the formation of meanders and eddies on larval fish assemblages and transport in this region was not possible to ascertain, and is not currently well known.

Larval fish assemblages were well correlated to seasonal environmental variables, such as air temperature, Leeuwin Current strength and sea surface temperature. While variables such as air temperature followed meteorological seasons, with minimum values in winter and maximum values in summer, oceanographic variables such as FMSL (i.e., the strength of the Leeuwin Current) were at a minimum in spring, and a maximum in autumn. These two seasonal cycles were reflected in larval fish

assemblage structure. However, while broad distinctions were able to be made between larval fish assemblages from different water masses, meteorological and oceanographic conditions (some on relatively short time-scales), were influential in further structuring larval fish assemblages. Some smaller-scale biological and meteorological processes correlated to assemblages included nitrate and nitrite concentrations, and microzooplankton concentrations. However, high microzooplankton concentrations were not generally found in association with high larval fish concentrations, especially when clupeiform larvae were considered. This suggested that the autumn/winter oceanographic regime associated with higher phytoplankton and microzooplankton biomass was not conducive to high rates of larval fish retention.

In this study, most larval fish assemblage analyses were completed using non-parametric, multivariate statistical methods, in the Primer-6 computer package. These methods were ideal for analysis of biological assemblage data, as the contribution of all sampled species to assemblage structure, not just a few common taxa, could be examined. These methods also did not have the problems associated with performing multiple univariate tests, such as increased chance of a Type 1 (false positive) error. Tests for statistical significance were completed using permutation testing, which circumvented the usual requirements of statistical tests for significance, such as t-tests or ANOVAs (normal distributions, equality of variance between groups) (Clarke and Warwick, 2001). Multivariate statistical methods thus proved to be highly appropriate and useful for this study, and were shown to generate robust results. Their use for analysis of larval fish assemblage data from other sources is to be recommended.

7.2 Recommendations for further research

This study represents the first comprehensive documentation of temporal and spatial structure in larval fish assemblages off south-western Australia. Sampling was at a monthly to quarterly temporal regime, on the scale of tens of kilometres. While larvae were collected from a range of teleost taxa with inshore, shelf and offshore habitat affiliations, there were some notable absentees within the larval fish assemblages examined. Larvae of some coastal and shelf species of commercial significance, such as *Glaucosoma herbraicum* (Dhufish), *Pagrus auratus* (Pink Snapper), *Pomatomus saltatrix* (Tailor), *Sillaginodes punctata* (King George Whiting) and *Arripus* spp. (Australian salmon, Australian herring) were all either absent or extremely rare in all samples. This suggests that the larval fish assemblages defined within this study, especially on the continental shelf, may be considered to represent a pelagic assemblage, with larvae from pelagic families (Clupeidae, Carangidae) prevalent. To gain information on the distributions of the species mentioned above, sampling on a finer scale, in and around local islands and embayments, may be preferable for the collection of these larvae. Species whose larvae were collected commonly, such as *S. sagax*, show a protracted spawning period, while species such as *G. herbraicum* and *P. auratus* have much shorter spawning periods (Hesp *et al.*, 2002; Moran *et al.*, 2003). To collect larvae of these species, sampling on a finer temporal scale may therefore also be required.

Larval fish assemblages described in this study showed strong spatial and temporal patterns of abundance, linked to water mass structure. However, environmental correlations suggested that finer-scale meteorological and biological variables may be influential on assemblage structure, and larval fish distributions. To explore this

further, sampling on a finer temporal and spatial scale would be necessary. Collecting samples every week, as opposed to every month, or in grid on a finer scale than a five-station 84km transect, or following a specific oceanographic feature may be necessary, depending on the research question being investigated. Conversely, if broad, regional patterns in larval fish assemblage structure are to be understood, sampling across a larger latitudinal extent of the coastline would be required.

Larval fish assemblages between two oceanic, mesoscale Leeuwin current eddies were compared, and related to oceanographic structures. However, because of the age of the eddies when they were sampled (about five months), it was not possible to ascertain the influence of eddy formation on larval fish entrainment and dispersal. To investigate this, targeted sampling of Leeuwin Current meanders and eddies as they form, in locations closer to the coast than sampled in this study, would be required.

The strength of the Leeuwin Current is known to vary with the El Niño cycle (Pearce, 1991). This variability has been correlated with recruitment to some regional fisheries, and subsequent catch rates (Lenanton *et al*., 1991; Caputi *et al*., 1996). This study was not of sufficient duration to consider the effects of such climatic variability on physical and biological conditions, and thus larval fish assemblages, although the strength and location of the Leeuwin Current was shown to influence larval advection and species distributions. To investigate this, and the mechanisms behind the observed correlations as they relate to larval fishes, would require collection of samples over a longer timescale. Future examination of the relationships between larval fish nutrition, growth and survival may also help to understand the interactions between larval fish and their environment, within the study region.

Overall, larval fish assemblages investigated in this study across the coastal, shelf and slope waters off south-western Australia showed strong spatial and temporal patterns. Much of the variability in assemblages was directly or indirectly attributable to regional oceanography, and water mass structure. The unique oceanography off south-western Australia thus has considerable implications for larval fish retention, survival, and subsequent recruitment to regional fisheries.

Appendices

Appendix 1: Species composition by month of all larval fish collected from bongo nets, August 2002 to December 2004 on the Two Rocks transect. Total number of individuals collected across all stations are shown.

Family/Order	Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Acanthuridae	Acanthuridae sp.1				1	**No**							
Acropomatidae	*Apogonops anomalous*	6	7	89	14	**samples**			3	2	5	47	105
Anopteridae	Anopteridae sp.1					**taken**							1
Aploactinidae	Aploactinidae sp.1				2		1						
Apogonidae	*Lachneratus* sp. 1			1	3								
	Apogonidae sp.1	22	69	9	5				6				45
	Apogonidae sp.2	2	2										
	Siphamia sp. 1		1		3								
	Apogonidae sp.3		1										
Arripidae	*Arripus* sp. 1				14		1		2				
Aulopidae	Aulopidae sp.1												2
Belonidae	Belonidae sp.1			1					2				
Beryciformes	Beryciformes spp.									1			1
Blenniidae	*Parablennius postoculomaculatus*	53	58	15	7			2	3	1	27	19	285
Bramidae	*Brama* sp. 1		2					1	1	1		1	
Bregmacerotidae	*Bregmaceros* spp.	1	1		14		1	7	6			1	56
Callionymidae	Callionymidae sp.1	24	35	27	39		4		3	24	18	45	54
Carangidae	Carangidae spp.	40	40	7	1		1		1			10	5
	Pseudocaranx spp.	9	26	178	10		4		2		24	10	48
	Trachurus novazelandiae	3	136	19	10			3					2
Carapidae	Carapidae sp.1								1	1			
Cepolidae	*Owstonia* sp. 1							1		1			
Ceratoidea	Ceratoidea sp.1				1			4					
Chaetodontidae	Chaetodontidae sp.1		2				1						
Champsodontidae	Champsodontidae sp.1				1								
Chauliodontidae	*Chauliodus sloani*				6			7	8	3	1	3	1
Cheilodactylidae	Cheilodactylidae sp.1		1						3				
Chiasmodontidae	*Kali macrura*								5	1			
Clinidae	Clinidae sp.1	26	40	10	9			18	109	69	39	43	186
Clupeidae	*Etrumeus teres*	36	80	30	50		29	18	27	12	130	21	205
	Sardinops sagax	199	289	59	374		141	29	571	20	240	71	362
	Spratelloides robustus	2	2	2					2	7	6	4	17
	Clupeiformes spp.	3	7	8	12		12		162	1	4		79
Creedidae	*Creedia haswellii*	2	46	76	36		2		3	1	26	132	42
	Limnichthys fasciatus		1	2							1	8	3
Cynoglossidae	Cynoglossidae spp.		2		2				4	3			
Dinolestidae	*Dinolestes lewinii*		1				1					2	
Engraulidae	*Engraulis australis*	12	59	41	457		56	20	1	1	25	196	325
Enoplosidae	*Enoplosis armatus*	1	1							1			
Epigonidae	Epigonidae sp.1								1				
Evermannellidae	*Evermannella* sp. 1		1					1					2
Exocoetidae	Exocoetidae sp.1												1
Gadiformes	Gadiformes spp.									1			
Gempylidae	*Rexea* sp. 1										1		4
Gerreidae	*Paraquella* sp. 1	2	5									3	1
Glaucosomatidae	*Glaucosoma herbraicum*												1

Family/Order	Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Gobiidae	*Afurcogobius suppositus*	24	66	7	3				2	4	48	43	103
	Gobiidae sp.1	162	321	98	16		2		2		4	41	181
	Gobiidae sp.2		1					2	4	1	1		28
Gobiesocidae	Gobiesocidae sp.1	21	21	9	5		1	7	10	2	2	30	21
	Alabes sp. 1	15	15					3	6	11	12	35	13
	Gobiesocidae sp.2	4	4						1	1	3	3	5
Gonorynchidae	*Gonorynchus greyii*				2			1		1			
Gonostomatidae	*Cyclothone* spp.	1	6	3	16			26	32	27	29		132
Idiacanthidae	*Idiacanthus anstrostomus*							4		2			
Kyphosidae	Kyphosidae sp.1			2	1					2			3
Labridae	Labridae sp.1	9	21		6				29	23	301	385	940
	Labridae sp.2	25	34	3	129		4		4			2	11
	Labridae sp.3	1	1		6			17	7	12	2	2	3
	Labridae sp.4	1	3									1	
	Labridae sp.5		2							15	3		9
	Labridae sp.6												3
	Labridae sp.7												11
Lampriformes	Lampriformes sp.1												1
Latidae	Latidae sp.1												
Melamphaeidae	Melamphidae spp							3		3		1	1
Melanostomiatidae	Melanostomiatidae sp.1		2		1			1					
Microdesmidae	Microdesmidae sp.1		1		1								
Monacanthidae	Monacanthidae spp.	16	33	7	3			9	8	24	24	119	158
Monodactylidae	*Schuettia woodwardii*	6	8	2	1								4
Moridae	Moridae spp.		2	2	4		6	22	66	18	16	6	8
Mullidae	Mullidae sp.1	8	14	1					1	4	33	19	62
Myctophidae	Unidentified		4	5	7			3	7	1	3		42
	Benthosema suborbitale			1	6			5	4		1	1	4
	Ceratoscopelus warmingii		1								13	3	75
	Centrobranchus sp. 1		2						2				2
	Diaphus "slender" spp.	125	309	92	489		130	88	52	34	13	3	65
	Diaphus "stubby" spp.	1	2		10		2						23
	Diogenichthys atlanticus	9	34	1	15			6	22	16	30	31	181
	Hygophum spp.		2	1	2		7	79	14	43	10	6	15
	Lampadena spp.	14	55	6	34		1	19	1	1	5	3	111
	Lampanyctus spp.	13	65	18	111		22	78	33	84	38	3	114
	Lampanyctus intricarius									1	4		
	Lobianchia dofleini							5	4	8			10
	Lobianchia gemellari								1				
	Myctophum asperum	5	7	10	23			1					42
	Myctophum phengodes		2	3				4	9	5	2	1	1
	Notoscopelus resplendens	1	2		2			12	3	5			4
	Nannobranchium achirus									1	1		
	Notolynchnus valdiviae				2								
	Scopelopsis multipunctatus		1				6	341	31	34		2	3
	Symbolophorus spp.	1	4					5	4	2	4	1	3
Nempiteridae	*Nemipterus* sp. 1	12	13										
Nomeidae	*Psenes whiteleggii*							1					
Notosudidae	*Scopelosaurus ahlstromi*			2	1			12	2				
Odacidae	Odacidae spp.	3	12						13	16	29	123	61
Opistognathidae	Opistognathidae sp.1												1
Ostraciidae	*Lactoria* sp. 1			1	2			1				1	
Paralepididae	Paralepididae spp.	4	5	1	4		2	8	1	3	3		2
Pempheridae	Pempheridae spp.	4	20	44	12				3	26	5	88	55
Percichthyidae	Percichthydae sp.1		1		2			2		3			2

Family/Order	Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Percophidae	*Enigmapercis reducta*	5	22	13	7					2	32	47	62
	Percophidae sp.1		1		1								1
Phosichthydae	*Vinciguerria* spp.	9	44	13	118		18	141	36	64	34	4	144
	Pollichthys sp. 1				6								
Pinguipedidae	*Parapercis* sp. 1	37	56	5	4		2		4	12	4	27	73
Platycephalidae	Platycephalidae sp.1	8	16	7	8		1				6	4	20
	Platycephalidae sp.2			9	1		1		2	1			5
	Platycephalidae sp.3								1				
Plesiopidae	*Beliops xanthokrossos*	2	2								2	3	10
	Paraplesiops sp. 1	2	6		1						1		2
	Plesiopidae sp.1			1									
Pleuronectiformes	Pleuronectiformes spp.	3	8	3	3			3	10	4	18	21	19
Pomacentridae	*Chromis* sp. 1	1	3	3	2			7					52
	Abudefduf sp. 1			3									
	Amphriopion sp. 1			1									
	Pomacentridae sp.1		2	8					1	6		8	19
	Pomacentridae sp.2	1	1									3	14
Pomatomatidae	*Pomatomus saltatrix*				1								
Scombridae	*Scomber australiscus*	5	15	35	9		6			1			15
Scopelarchidae	*Scopelarchus* sp. 1		1		11			1	1				3
Scorpaenidae	Scorpaenidae sp.1	2	2		1			5	55	52	9	2	4
	Scorpaenidae sp.2	1	2		17			1			1	9	16
	Scorpaenidae sp.3	3	4	9	16								1
	Scorpaenidae sp.4	6	15	26	13		2	2	11	9	4	8	14
Scorpididae	Scorpididae sp.1								2				
Serranidae	*Hypoplectrodes* sp. 1		5	9	2				6	1		1	4
Sillaginidae	*Sillago* spp.	18	25	1				4	6	1	6	16	26
Sparidae	Sparidae sp.1	4	6	1								3	2
Sphyraenidae	Sphyraenidae sp.1		8										1
Stomiiformes	Stomiiformes sp.1				1				4				1
Stromateoidei	Stromateoidei sp.1								1				
Syngnathidae	Syngnathidae sp.1	3	4	4	3					2	2	6	2
	Syngnathidae sp.2	2	4	1	1				1	1	2	1	2
	Syngnathidae sp.3											1	1
Synodontidae	Synodontidae sp.1			1			2						
Terapontidae	Terapontidae sp.1	16	16									2	10
Tetraodontidae	Tetraodontidae sp.1	93	117	1							4	7	217
Trachichthydae	Trachichthydae sp.1				4				2			4	
Triglidae	Triglidae sp.1									4	1	4	6
Tripterygiidae	Tripterygiidae sp.1	46	64	36	67			4	4	3	33	67	304
Uranoscopidae	Uranoscopidae sp.1		1		1								
Zeidae	Zeidae sp.1												1

Appendix 2A: Environmental variables and values for all stations and samples across the Two Rocks transect, August 2002 to December 2004: Physicochemical variables. Sources: SRFME, National Tidal Centre, A. Pearce.

	Fremantle Mean Sea Level (cm)	FMSL anomaly (cm)	Sea surface temperature (°C)	Surface salinity	NO_x at surface (µmoles/L)
August 02_A	71.7	9.6	16.24	35.38	1.27
August 02_B	71.7	9.6	18.56	35.46	0.07
August 02_C	71.7	9.6	19.21	35.42	0.14
August 02_D	71.7	9.6	19.84	35.41	0.00
August 02_E	71.7	9.6	19.76	35.39	0.14
November 02_A	55.5	2.4	20.25	35.67	0.09
November 02_B	55.5	2.4	19.19	35.71	0.03
November 02_C	55.5	2.4	18.93	35.70	0.07
December 02_A	64.4	10.2	21.25	35.88	0.16
December 02_B	64.4	10.2	20.50	35.79	0.04
December 02_D	64.4	10.2	20.85	35.65	0.07
December 02_E	64.4	10.2	21.05	35.72	0.04
February 03_A	73.7	16.4	23.50	36.42	0.00
February 03_B	73.7	16.4	21.78	35.88	0.02
February 03_C	73.7	16.4	23.06	35.61	0.00
February 03_D	73.7	16.4	22.82	35.60	0.00
February 03_E	73.7	16.4	22.82	35.58	0.00
March 03_A	76.6	15.9	22.87	36.28	0.77
March 03_B	76.6	15.9	22.85	35.64	0.00
March 03_C	76.6	15.9	23.34	35.59	0.00
April 03_A	81.3	14.9	21.12	36.01	1.67
April 03_B	81.3	14.9	21.71	35.72	0.51
April 03_C	81.3	14.9	22.16	35.58	0.17
April 03_D	81.3	14.9	22.58	35.53	0.17
April 03_E	81.3	14.9	22.42	35.54	0.37
June 03_A	87.9	13.5	20.02	35.51	0.03
June 03_B	87.9	13.5	21.12	35.49	0.00
June 03_C	87.9	13.5	22.00	35.45	0.00
July 03_A	76.7	8.0	16.90	35.47	1.25
August 03_A	73.6	11.4	16.19	35.40	0.95
August 03_B	73.6	11.4	17.76	35.67	0.07
August 03_C	73.6	11.4	19.71	35.65	0.26
August 03_D	73.6	11.4	19.40	35.59	0.13
August 03_E	73.6	11.4	16.98	35.71	0.01
December 03_A	64.5	10.2	20.43	35.75	0.21
December 03_B	64.5	10.2	19.96	35.73	0.01
December 03_C	64.5	10.2	19.62	35.73	0.00
December 03_D	64.5	10.2	20.02	35.65	0.00
December 03_E	64.5	10.2	19.90	35.66	0.00
January 04_A	67.5	13.2	20.70	35.92	0.27
January 04_B	67.5	13.2	20.39	35.86	0.19
January 04_C	67.5	13.2	20.52	35.80	0.39
January 04_D	67.5	13.2	21.11	35.78	0.00
January 04_E	67.5	13.2	21.44	35.78	0.16
March 04_A	68.1	7.3	21.13	36.31	1.03
March 04_B	68.1	7.3	21.01	36.00	0.04
March 04_C	68.1	7.3	21.91	35.72	0.01
April 04_A	81.9	15.4	20.99	36.20	1.35
April 04_E	81.9	15.4	20.10	35.70	0.02

	Fremantle Mean Sea Level (cm)	FMSL anomaly (cm)	Sea surface temperature (°C)	Surface salinity	NO_x at surface (μmoles/L)
June 04_A	89.6	15.1	20.64	35.51	0.48
June 04_B	89.6	15.1	21.33	35.48	0.12
June 04_C	89.6	15.1	17.38	35.49	0.47
July 04_A	81.9	13	19.49	35.50	1.45
July 04_B	81.9	13	20.25	35.56	0.11
July 04_C	81.9	13	19.55	35.56	0.33
July 04_D	81.9	13	20.09	35.70	0.00
July 04_E	81.9	13	16.74	35.69	0.01
August 04_A	69.2	6.8	18.99	35.55	1.14
August 04_C	69.2	6.8	19.70	35.58	0.05
September 04_A	64.4	8.6	17.41	25.64	0.08
September 04_B	64.4	8.6	18.47	35.65	0.00
September 04_C	64.4	8.6	18.88	35.66	0.01
September 04_D	64.4	8.6	18.75	35.67	0.00
September 04_E	64.4	8.6	18.36	35.77	0.00
October 04_A	65.1	11.8	19.28	35.71	0.48
October 04_B	65.1	11.8	18.93	35.76	0.00
October 04_C	65.1	11.8	18.50	35.78	0.02
November 04_A	72	18.7	20.47	35.86	0.47
November 04_B	72	18.7	20.20	35.82	0.04
November 04_C	72	18.7	20.13	35.79	0.02
December 04_A	69.8	15.4	22.39	36.03	0.74
December 04_B	69.8	15.4	21.61	35.91	0.00
December 04_C	69.8	15.4	21.09	35.74	0.05
December 04_D	69.8	15.4	21.27	35.65	0.00
December 04_E	69.8	15.4	21.70	35.67	0.01

Appendix 2B: Environmental variables and values for all stations and samples across the Two Rocks transect, August 2002 to December 2004: Meteorological and biological variables. Meteorological variables represent a mean for the five days prior to sampling. Sources: SRFME, Western Australian Bureau of Meteorology, S. Pesant, Paterson (2006).

	Maximum air temperature (°C)	Solar radiation (MJ/m^2)	Mean wind speed (m/s)	Wind direction (from) (°)	Maximum chlorophyll (mg $/m^3$)	Chlorophyll α: surface (mg/m^3)	Microzoo-plankton no./L: surface	Microzoo-plankton no. /L: CM
August 02_A	17.7	15.4	8.59	197	0.24	0.4	2 569.41	1 800.00
August 02_B	17.7	15.4	8.59	197	0.70	0.59	2 094.12	1 447.06
August 02_C	17.7	15.4	8.59	197	0.80	0.75	2 800.00	2 296.47
August 02_D	18.4	15.8	8.39	215	0.65	0.27	5 341.18	1 352.94
August 02_E	17.7	15.4	8.59	197	0.64	0.59	2 705.88	2 529.41
November 02_A	25.2	28.4	9.25	221	0.24	0.44	1 438.82	1 305.88
November 02_B	25.2	28.4	9.25	221	0.34	0.34	1 470.59	1 863.53
November 02_C	25.2	28.4	9.25	221	0.42	1.71	1 188.24	1 129.41
December 02_A	24.3	27	7.7	157	0.69	0.5	1 776.47	1 882.35
December 02_B	24.3	27	7.7	157	0.69	0.22	1 301.18	2 857.65
December 02_D	23.9	25.8	6.83	130	0.41	0.03	823.53	1 176.47
December 02_E	23.9	25.8	6.83	130	0.65	0.04	1 482.35	1 000.00
February 03_A	29.6	27	7.47	146	0.56	0.53	2 331.76	4 988.24
February 03_B	29.5	24.6	7.9	126	0.28	0.07	1 047.06	1 952.94
February 03_C	29.6	27	7.47	146	0.69	0.09	1 937.65	4 082.35
February 03_D	29.3	27.6	7.9	137	0.56	0.07	2 668.24	2 188.24
February 03_E	29.3	27.6	7.9	137	0.36	0.13	2 058.82	2 105.88
March 03_A	24	15.2	5.4	189	0.98	1.14	10 541.18	2 447.06
March 03_B	24	15.2	5.4	189	0.76	0.58	1 423.53	1 294.12
March 03_C	24	15.2	5.4	189	0.55	0.38	1 258.82	1 741.18
April 03_A	20.5	13.8	5.99	177	1.21	1.15	2 350.88	1 407.56
April 03_B	21	15.6	6.77	225	0.60	0.59	2 026.89	1 588.24
April 03_C	21	15.6	6.77	225	0.74	0.62	1 517.65	1 988.24
April 03_D	21	15.6	6.77	225	0.57	0.25	1 329.41	905.88
April 03_E	22.3	15.6	7.07	254	0.61	0.61	1 847.06	2 082.35
June 03_A	19.5	11	5.58	200	0.56	0.77	5 726.30	3 783.53
June 03_B	19.5	11	5.58	200	0.83	1.05	5 838.78	1 611.76
June 03_C	19.5	11	5.58	200	0.55	0.99	1 811.76	764.71
July 03_A	17.8	9	8.76	106	0.22	0.26	3 625.70	400.00
August 03_A	16.1	10.8	10.13	135	0.83	1.08	7 778.88	1 365.23
August 03_B	16.1	11.8	10.29	124	1.55	1.51	5 374.85	1 213.54
August 03_C	16.1	10.8	10.13	135	1.04	0.81	4 154.03	2 637.11
August 03_D	16.7	14.2	8.37	197	1.00	1.07	2 380.40	1 610.27
August 03_E	17.6	14.2	5.92	242	1.11	0.55	2 108.77	3 411.76
December 03_A	23.1	28	9.02	162	0.26	0.45	3 104.61	3 020.13
December 03_B	24.5	28	8.3	202	0.23	0.13	3 564.71	2 658.82
December 03_C	23.1	28	9.02	162	0.49	0.12	1 788.08	3 908.33
December 03_D	24.5	28	8.3	202	0.40	0.27	2 537.88	1 564.71
December 03_E	23.4	29.6	8.04	162	0.74	0.31	1 576.47	2 794.65
January 04_A	24.3	28	9.31	137	0.66	0.78	3 513.51	3 515.45
January 04_B	24.3	28	9.31	137	0.24	0.15	1 033.25	1 547.48
January 04_C	22.8	27.6	10.05	119	0.62	0.1	2 074.41	3 137.70
January 04_D	24.2	28.4	8.3	167	0.69	0.13	3 919.61	2 938.69

	Maximum air temperature (°C)	Solar radiation (MJ/m^2)	Mean wind speed (m/s)	Wind direction (from) (°)	Maximum chlorophyll (mg/m^3)	Chlorophyll α: surface (mg/m^3)	Microzoo-plankton cells/L: surface	Microzoo-plankton cells /L: CM
January 04_E	25.1	27.8	7.16	153	0.63	0.25	1 885.71	2 370.37
March 04_A	26.2	15.8	7.48	207	0.66	0.36	1 749.14	851.55
March 04_B	26.2	15.8	7.48	207	0.91	0.78	1 880.14	1 710.53
March 04_C	26.2	15.8	7.48	207	0.55	0.17	2 453.70	1 443.91
April 04_A	23.3	14.2	7.12	169	0.51	0.49	2 152.94	952.94
April 04_E	24.4	12.8	5.85	178	0.29	0.1	1 270.59	1 929.41
June 04_A	20.3	9.4	6.29	149	0.89	0.2	7 152.20	3 372.60
June 04_B	20.3	9.4	6.29	149	0.90	0.62	11 019.74	4 868.20
June 04_C	20.3	9.4	6.29	149	0.25	0.73	3 000.00	1 779.36
July 04_A	18	11.8	6.81	241	1.24	0.23	2 052.69	2 591.77
July 04_B	18.1	13.4	6.18	252	0.49	1.26	2 534.72	2 714.62
July 04_C	18.1	13.4	6.18	252	0.47	0.36	2 164.35	2 235.02
July 04_D	18.1	13.4	6.18	252	0.73	0.24	4 133.41	1 608.15
July 04_E	17.8	13.2	6.01	261	0.29	0.44	2 056.96	3 318.49
August 04_A	16.6	13.8	5.97	206	0.86	0.17	4 422.88	904.08
August 04_C	16.6	13.8	5.97	206	0.64	0.59	3 699.55	2 563.51
September 04_A	18.2	18	3.82	164	0.47	0.42	3 584.27	3 242.94
September 04_B	18.2	18	3.82	164	0.82	0.29	1 957.45	3 362.35
September 04_C	18.2	18	3.82	164	0.41	0.32	1 148.65	678.16
September 04_D	18.2	18	3.82	164	0.69	0.18	1 334.09	2 033.71
September 04_E	18.2	18	3.82	164	0.97	0.05	821.92	995.48
October 04_A	23.1	25.2	8.88	234	0.33	0.12	1 266.38	993.23
October 04_B	23.1	25.2	8.88	234	0.39	0.24	747.77	834.25
October 04_C	23.1	25.2	8.88	234	0.50	0.15	830.6	1 270.90
November 04_A	22.3	25.2	8.76	148	0.27	0.22	102.48	1 446.91
November 04_B	22.3	25.2	8.76	148	0.27	0.36	834.26	567.3
November 04_C	22.3	25.2	8.76	148	0.54	0.13	772.78	1 068.08
December 04_A	27.5	25.6	7.12	131	0.30	0.34	3 776.47	2 611.76
December 04_B	27.1	28.8	7.12	135	0.29	0.45	2 247.06	1 329.41
December 04_C	27.1	28.8	8.45	135	1.08	0.52	1 257.56	2 086.17
December 04_D	27.1	28.8	6.82	135	0.51	0.31	776.05	1 325.58
December 04_E	27.1	28.8	8.87	135	0.78	0.05	803.66	1 103.45

Appendix 3A: Mean concentrations (number/m^3) of *Sardinops sagax* and *Etrumeus teres* collected from August 2002 to December 2004 on the Two Rocks transect, at all sampling stations. "p" denotes larvae present at less than 0.01 per m^3.

	Sardinops sagax					*Etrumeus teres*				
Station	**Stn A (18m)**	**Stn B (40m)**	**Stn C (100m)**	**Stn D (300m)**	**Stn E (1000m)**	**Stn A (18m)**	**Stn B (40m)**	**Stn C (100m)**	**Stn D (300m)**	**Stn E (1000m)**
Aug-02		1.17	0.19	0.04	p		0.03		0.02	p
Nov-02		0.01	0.06					0.04		
Dec-02	0.03	p	p	p		p	p	0.06		
Jan-03	0.02									
Feb-03	0.01	0.39		p			0.11	0.07		
Mar-03	p	0.11	0.02			p	0.07			
Apr-03		0.25	0.37	0.02	0.01	p	0.05	0.03	0.01	
Jun-03	0.1	0.05	0.2			0.01	0.01	0.05		
Jul-03	p									
Aug-03		0.38	0.01	0.02				0.01	p	
Sep-03		0.01	0.01				0.01	p		
Oct-03	p	0.01	0.03					0.01		
Nov-03		0.02	0.04	p				0.02		
Dec-03		0.02	0.27		0.02		0.03	0.28		0.03
Jan-04	0.09	0.31	0.17	0.02	0.02		0.01	0.14	0.01	
Mar-04	0.01	0.13	0.01				0.05	0.01		
Apr-04	p			p		p				
Jun-04	0.01	0.01	0.05					0.01		
Jul-04		0.06	0.02				0.08	0.01		
Aug-04			0.01					0.02		
Sep-04		0.06					0.02	0.01		
Oct-04		0.28	0.73				0.06	0.42		
Nov-04		0.07	0.11				0.03	0.04		
Dec-04		0.27	0.11	p			0.04	0.05	0.01	

Appendix 3B: Mean concentrations (number/m^3) of *Engraulis australis* and *Spratelloides robustus* collected from August 2002 to December 2004 on the Two Rocks transect, at all sampling stations. "p" denotes larvae present at less than 0.01 per m^3.

	Engraulis australis					*Spratelloides robustus*				
Station	**Stn A (18m)**	**Stn B (40m)**	**Stn C (100m)**	**Stn D (300m)**	**Stn E (1000m)**	**Stn A (18m)**	**Stn B (40m)**	**Stn C (100m)**	**Stn D (300m)**	**Stn E (1000m)**
Aug-02				p						
Nov-02										
Dec-02	0.01	0.47	0.03							
Jan-03	0.02									
Feb-03	0.02	0.19								
Mar-03	0.1					p				
Apr-03	0.03	0.33	0.44	0.01	0.01					
Jun-03	0.06	0.09	0.01							
Jul-03	p									
Aug-03							p			
Sep-03						0.02				
Oct-03	p	0.04	p	p		0.02				
Nov-03			0.01			0.02				
Dec-03		0.16	0.12		0.01	0.07				
Jan-04	p	0.01			0.02	0.01				
Mar-04	0.02	0.05				0.01				
Apr-04				p						
Jun-04	0.01		0.01							
Jul-04		0.1	p							
Aug-04						0.01				
Sep-04	0.01					0.02	0.01			
Oct-04	0.02	0.21	0.01							
Nov-04		1.01	0.08			0.01				
Dec-04	0.02	0.02	0.04			0.07				

Appendix 4: Species list and number of larval fish specimens collected in the eastern Indian Ocean in the warm-core (WC) and cold-core (CC) eddies by bongo and EZ nets.

Family	Species	WC bongo	CC bongo	WC EZ	CC EZ
Anguilliformes	Unidentified	4	9	12	11
Stomiiformes	Unidentified			2	3
Gonostomatidae	*Cyclothone* spp.	25	117	48	137
	Margrethia sp.			2	
Phosichthydae	*Vinciguerria* spp.	73	246	100	174
	Ichthyococcus sp.		1		
Chauliodontidae	*Chauliodus sloani*	13	25	45	66
Sternoptychidae	*Argyropelecus* spp.	2	2	19	
	Sternoptyx sp.		2	3	2
	Polyipnus sp.			1	
	Valenciennellus sp.			4	3
	Unidentified	1	2	3	13
Stomiidae	*Astronesthes* sp.				1
	Melanostomias sp.		2		
Melanostomiatidae	Unidentified			1	
Notosudidae	Unidentified			1	1
Evermannellidae	*Evermannella* sp.		1	1	2
Paralepididae	Unidentified	1	2	2	
Scopelarchidae	*Lestrolepis* sp.	4	6	1	11
	Macroparalepis sp.		1		
	Unidentified	2	4	8	21
Myctophidae	*Benthosema suborbitale*		10	15	8
	Centrobranchus andreae				1
	Centrobranchus nigroocellatus		3		2
	Ceratoscopelus warmingii	6	65	1	2
	*Diaphus "slender"*spp.	9	16	11	6
	Diogenichthys atlanticus	102	247	218	165
	Electrona risso				1
	Hygophum sp.		1	17	2
	Hygophum "B"	12	9	24	6
	Hygophum hygomii	25	30	40	16
	Hygophum proximum	2		3	
	Lampadena sp.		2	3	4
	Lampadena luminosa	5	4	8	
	Lampanyctus spp.	3	35	4	2
	Lampanyctus "B"	5	1	4	1
	Lampanyctus australis/alatus	28	18	40	1
	Lampanyctus intricarius	13	7	10	3
	Lampanyctus pusillus	12	6	1	
	Lampanyctus "steinbecki" type		9	24	
	Lobianchia doflieni	29	10	25	6
	Lobianchia gemellarii	2			1
	Myctophum sp.		1	6	5
	Myctophum asperum	1			
	Myctophum aurolanternatum		1		
	Myctophum phengodes	17	37	35	5
	Myctophum spinosum			2	
	Nannobranchium achirus	2	3		
	Notolynchnus valdiviae		4		
	Notoscopelus respendens	19	23	49	16
	Promyctophum (Hierops) sp.	2	5	4	
	Scopelopsis multipunctatus	7	5	10	2
	Symbolophorus sp.	4	4		
	Symbolophorus evermanni	4	3	4	1
	Unidentified	6	18	63	64
Gadiformes	Unidentified		1	1	
Ceratiidae	Unidentified	1	1	4	5
Hemiramphidae	Unidentified	4	2	4	
Exocoetidae	Unidentified		1		
Melamphaeidae	Unidentified	6	13	4	4
Centriscidae	*Macroramphosus* sp.		1		
Scorpaenidae	Unidentified	1	1	10	
Howellidae	*Howella* sp.	1	11	9	2
Bramidae	*Brama* sp.	3	2	6	
Labridae	Unidentified	1	1	3	1
Chiasmodontidae	*Kali macrura*	2	1	4	
TOTAL		459	1032	919	777

Appendix 5: Abundance of late juvenile and adult stages of Myctophidae fishes in the warm-core (WC), and cold-core (CC) eddies, sampled with bongo and EZ nets.

Species	WC Centre	WC Body	WC Perimeter	CC Centre	CC Body	CC perimeter
Benthosema suborbitale	2				1	
Bolinichthys indicus				1		1
Bolinichthys photothorax					1	
Ceratoscopelus warmingii			2		2	1
Diogenichthys atlanticus				1	2	2
Diaphus spp.	2				3	1
Electrona risso						1
Hygophum hygomii		3	1		1	
Hygophum spp.	1	1		1		
Lampanyctus alatus	10	7	3	11	4	4
Lampanyctus australis				3		
Lampanyctus pussilus						1
Lampanyctus spp.				1		2
Lobianchia sp.		1				
Myctophum phengodes	1					
Notolynchnus valdiviae			1			
Promyctophum subparallellum			1			
Scopelopsis multipunctatus	1	1	1	5	8	1
Symbolophorus sp.					1	

References

Ahlstrom, E. H., 1959. Vertical distribution of pelagic fish eggs and larvae, off California and Baja California. Fishery Bulletin 60, 107-146.

Ahlstrom, E. H., 1969. Mesopelagic and bathypelagic fishes in the California Current region. CalCOFI Report 13, 5pp.

Andrews, W. R. H., Hutchings, L. 1980. Upwelling in the southern Benguela Current. Progress in Oceanography 9, 1-81.

Armsworth, P. R., 2001. Directed motion in the sea: efficient swimming by reef fish larvae. Journal of Theoretical Biology 210, 81-91.

Avalos-Garcia, C., Sanchez-Velaso, L., Shirasago, B., 2003. Larval fish assemblages in the Gulf of California and their relation to hydrographic variability (autumn 1997-summer 1998). Bulletin of Marine Science 72, 63-76.

Bailey, K. M., 1981. Larval transport and recruitment of Pacific Hake *Merluccius productus*. Marine Ecology Progress Series 6, 1-9.

Bailey, K. M., Houde, E. D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Science 25, 1-83.

Bakun, A., 1985. Comparative studies and the recruitment problem: searching for generalisations. CalCOFI Report 26, 11pp.

Bakun, A., 1996. Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Grant College System, University of California, La Jolla, 323pp.

Batten, S. D., Crawford, W. R., 2005. The influence of coastal origin eddies on oceanic plankton distributions in the eastern Gulf of Alaska. Deep Sea Research Part 2 52, 991-1009.

Baumann, H., Hinrichsen, H-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L. W., Temming, A. in press. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fisheries Oceanography.

Baumgaratner, T.R., Soutar, A., Ferreira-Bartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara basin, California. CalCOFI Reports 33: 24 – 30.

Beckley, L. E., van Ballegooyen, R.C., 1992. Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. South African Journal of Marine Science 12, 83-93.

Beckley, L. E., Hewitson, J. D. 1994. Distribution and abundance of clupeiod larvae along the east coast of South Africa in 1990/91. South African Journal of Marine Science 14, 205-212.

Beckley, L. E., van der Lingen, C., 1999. Biology, fishery and management of sardines (*Sardinops sagax*) in southern African waters. Marine and Freshwater Research 50, 955-978.

Bergeron, J.-P., 2000. Effects of strong winds on the nutritional condition of anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay, Northeast Atlantic, as inferred from an early field application of the DNA/-index. ICES Journal of Marine Science 57, 249-255.

Bjork, G., Nordberg, K., 2003. Upwelling along the Swedish west coast during the 20th century. Continental Shelf Research 23, 1143-1159.

Brandt, S. A., 1981. Effects of a warm-core eddy on fish distributions in the Tasman Sea off east Australia. Marine Ecology Progress Series 6, 19-33.

Brewer, G. D., Kleppel, G. S., 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Marine Ecology Progress Series 27, 217-226.

Brothers, E. B., Williams, D. M., Sale, P. F., 1983. Length of larval life in twelve families of fishes at One Tree Lagoon, Great Barrier Reef, Australia. Marine Biology 76, 319-324.

Brown, P. C., Field, J. G., 1986. Factors limiting phytoplankton production in a nearshore upwelling area. Journal of Plankton Research 8(1), 55-68.

Bruce, B. D., Evans, K., Sutton, C. A., Young, J. W., Furlani, D. M., 2001. Influence of mesoscale oceanographic processes on larval distribution and stock structure in Jackass Morwong (*Nemadactylus macropterus*: Cheilodactylidae). ICES Journal of Marine Science 58, 1072-1080.

Caputi, N., Fletcher, W. J., Pearce, A. F., Chubb, C. F., 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. Marine and Freshwater Research 47, 147-155.

Chambers, R. C., Trippel, E. A., 1997. Early life history and recruitment in fish populations. Chapman and Hall, 596pp.

Checkley, D. M., Raman, S., Maillet, G., Mason, K. M., 1988. Winter storm effects on the spawning and larval drift of a pelagic fish. Nature 355 (6188), 346-348.

Chisholm, W., 2004. Spatial and temporal distribution of *Pomatomus saltatrix* larvae off Western Australia. Honours thesis, School of Environmental Science, Murdoch University, Western Australia, 75pp.

Clarke, K. R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205-219.

Clarke, K. R., Warwick, R. M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd Edition, Natural Environment Research Council, Plymouth, .

Clarke, K. R., Warwick, R. M., 2005. Primer-6 Computer Program, Natural Environment Research Council, Plymouth.

Cole, J., 1999. Environmental conditions, satellite imagery, and clupeoid recruitment in the northern Benguela upwelling system. Fisheries Oceanography 8(1), 25-38.

Coombs, S. H., Giovanardi, O., Halliday, N. C., Francheschini, G., Conway, D. V. P., Manzueto, L., Barrett, C. D., McFadzen, I. R. B., 2003. Wind mixing, food availability and mortality of anchovy larvae *Engraulis encrasicolus* in the northern Adriatic Sea. Marine Ecology Progress Series 248, 221-235.

Cossington, S. 2006. The biology of the Foxfish *Bodianus frenchii* in the marine coastal waters of south-western Australia. Honours thesis, School of Biological Sciences, Murdoch University, Western Australia.

Cowen, R. K., Hare, J. A., Fahay, M. P., 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight? Bulletin of Marine Science 53(2), 567-587.

Cowen, R., 2002. Larval dispersal and retention and consequences for population connectivity. In: Coral Reef Fishes: Dynamics and diversity in a complex ecosystem (Sale, P. F. ed), pp. 149-170, Academic Press, London, New York.

Cowen, R., Paris, C. B., Olson, D. B., Fortuna, J. L., 2003. The role of long distance dispersal versus local retention in replenishing marine populations. Proceedings of the Gulf and Caribbean Fisheries Institute. 54, 789-790.

Cresswell, G. R., 1991. The Leeuwin Current - observations and recent models. Journal of the Royal Society of Western Australia 74, 1-14.

Cresswell, G. R., Griffin, D., 2004. The Leeuwin Current, eddies and sub-Antarctic waters off south-western Australia. Marine and Freshwater Research 55, 267-276.

Cubillos, L. A., Arcos, D. F., 2002. Recruitment of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central-south Chile in the 1990s and the impact of the 1997-1998 El Niño. Aquatic Living Resources 15, 87-94.

Cudaback, C. N., Largier, J. L., 2001. The cross-shelf structure of wind- and buoyancy-driven circulation over the North Carolina inner shelf. Continental Shelf Research 21, 1649-1668.

Curtis, K. A., 2004. Fine scale spatial pattern of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) eggs. Fisheries Oceanography 13, 239-254.

Cushing, D. H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology. 26, 249-293.

DeVlamming, V., Grossman, G., Chapman, F., 1982. On the use of the gonosomatic index. Comparative Biochemistry and Physiology 73,31–39.

Dickey-Collas, M., Gowen, R. J., Foz, C. J., 1996. Distribution of larval and juvenile fish in the Western Irish Sea: relationship to phytoplankton, zooplankton

biomass and recurrent physical features. Marine and Freshwater Research 47, 169-181.

Dimmlich, W. F., Breed, W. G., Geddes, M., Ward, T. M., 2004. Relative importance of gulf and shelf waters for spawning and recruitment of Australian anchovy, *Engraulis australis*, in South Australia. Fisheries Oceanography 13, 310-323.

Doyle, M. J., Morse, W. W., Kendall, A. W., 1993. A comparison of larval fish assemblages in the temperate zone of the Northeast Pacific and Northwest Atlantic Oceans. Bulletin of Marine Science 53, 588-644.

Echevin, V., Aumont, O., Tam, J., Pasapera, J., 2004. The seasonal cycle of surface chlorophyll along the Peruvian coast: Comparison between SeaWiFS satellite observations and dynamical/biogeochemical coupled model simulations. Gayana Concepcion 68(2), 325-326.

Espinosa-Fuentes, M. L., Flores-Coto, C., 2004. Cross-shelf and vertical structure of ichthyoplankton assemblages in continental shelf waters of the Southern Gulf of Mexico. Estuarine, Coastal and Shelf Science 59, 333-352.

Fairclough, D., 2005. The biology of four tuskfish species (Choerodon: Labridae) in Western Australia. PhD thesis, School of Biological Sciences, Murdoch University, Western Australia. 195pp.

Fandry, C. B., Slawinski, D., Pender, L. 2006. Two-Rocks moorings data report. CSIRO Marine and Atmospheric Research Paper 005, 26pp.

Fang, F., Morrow, R., 2003. Evolution, movement and decay of warm-core Leeuwin Current eddies. Deep Sea Research Part 2 50 (12-13), 2245-2261.

Fearns, P. R., Twomey, L., Zakiyah, U., Helleren, S., Vincent, W., Lynch, M.J., submitted. The Hillarys transect (3): Optical and chlorophyll relationships across the continental shelf off Perth. Continental Shelf Research.

Feng, M., Li, Y., Meyers, G., 2004. Multidecadal variations of Fremantle sea level: Footprint of climate variability in the tropical Pacific. Geophysical Research Letters 31(16): L16302.

Feng, M., Wijffels, S., Godfrey, S., Meyers, G. 2005. Do eddies play a role in the momentum balance of the Leeuwin Current? Journal of Physical Oceanography 35 (6), 964-976.

Feng, M., Fandry, C. B., Majewski, L., Waite, A. M., submitted. Physical characterisation of an eddy pair in the Leeuwin Current system off the western Australian coast. Deep Sea Research Part 2.

Fisher, R., Bellwood, D. R., 2002. A light trap design for stratum-specific sampling of reef fish larvae. Journal of Experimental Marine Biology and Ecology 269, 27-37.

Fisher, R., 2005. Swimming speeds of larval coral reef fishes: impacts on self-recruitment and dispersal. Marine Ecology Progress Series 285, 223-232.

Fisher, R., Leis, J. M., Clark, D. L., Wilson, S. K., 2005. Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. Marine Biology 147, 1201-1212.

Fletcher, W. J., 1990. A synopsis of the biology and exploitation of the Australian pilchard, *Sardinops neopilchardus* (Steindachner). Part 1. Biology. Western Australian Department of Fisheries, Fisheries Research Report 88. 45pp.

Fletcher, W. J., Tregonning R. J., 1992. Distribution and timing of spawning by the Australian pilchard (*Sardinops sagax neopilchardus*) off Albany, Western Australia. Australian Journal of Marine and Freshwater Research 43, 1437-1449.

Fletcher, W. J., Tregonning, R. J., Sant, G. J., 1994. Interseasonal variation in the transport of pilchard eggs and larvae off southern Western Australia. Marine Ecology Progress Series 111, 209-224.

Fletcher, W. J., 1999. Vertical distribution of pilchard (*Sardinops sagax*) eggs and larvae off Southern Australia. Marine and Freshwater Research 50, 117-22.

FAO (Food and Agriculture Organisation), 2004. Marine fisheries catch data: Clupeiformes. Accessed April 2006: www.fao.org.au/figis.

Franco-Gordo, C., Suarez-Morales, E., Godinez-Dominguez, E., Flores-Vargas, R., 2001. A seasonal survey of the fish larvae community of the central Pacific coastal of Mexico. Bulletin of Marine Science 68, 383-396.

Froese, R. 1990. Growth strategies of fish larvae. ICES C.M./L:91, 20pp.

Funes-Rodriguez, R., Hinojosa-Medina, A., Avendano-Ibarra, R., Hernandez-Rivas, M., Saldierna-Martinez, R., Watson, W., 2001. Spawning of small pelagic fishes in Bahia Magdalena Baja California Sur, Mexico, at the beginning of the 1997-1998 El Niño. Estuarine, Coastal and Shelf Science 53, 653-664.

Gallucci, F., Netto, S. A., 2004. Effects of the passage of cold fronts over a coastal site: an ecosystem approach. Marine Ecology Progress Series 281, 79-92.

Gartner, J. V., 1993. Patterns of reproduction in the dominant lanternfish species (Pisces: Myctophidae) of the eastern Gulf of Mexico, with a review of

reproduction among tropical-subtropical Myctophidae. Bulletin of Marine Science 52(2), 721-750.

Gaughan, D. J., Neira, F. J., Beckley, L. E., Potter, I. C., 1990. Composition, seasonality and distribution of the ichthyoplankton in the lower Swan Estuary, south-western Australia. Australian Journal of Marine and Freshwater Research 41, 529-543.

Gaughan, D. J., Fletcher, W. J., White, K. V., 2001a. Growth rate of larval *Sardinops sagax* from ecosystems with different levels of productivity. Marine Biology 139, 831-837.

Gaughan, D. J., White, K. V., Fletcher, W. J., 2001b. The links between functionally distinct adult assemblages of *Sardinops sagax*: larval advection across management boundaries. ICES Journal of Marine Science 58, 597-606.

Gaughan, D. J., Baudains, G. A., Mitchell, R. W. D., Leary, T. I. 2001c. Pilchard (*Sardinops sagax*) nursery areas and recruitment process assessment between different regions in southern Western Australia. Fisheries Research Report 131, Department of Fisheries, Western Australia, 48pp.

Gaughan, D. J., Leary, T. I., Mitchell, R. W., Wright, I. W., 2004. A sudden collapse in distribution of Pacific sardine (*Sardinops sagax*) off south-western Australia enables an objective reassessment of biomass estimates. Fishery Bulletin 102, 617-633.

Gaughan, D. J., Pearce, A. F., Lewis, P. D., submitted. The Hillarys transect: Influences on the dominant macrozooplankton and spawning of *Sardinops sagax* on the continental shelf off Perth, Western Australia. Continental Shelf Research.

Gersbach, G. H., Pattiaratchi, C., Ivey, G. N., Cresswell, G. R., 1999. Upwelling on the south-west coast of Australia - source of the Capes Current? Continental Shelf Research 19, 363-400.

Godfrey, J. S., Golding, T. J., 1981. The Sverdrup relation in the Indian Ocean, and the effect of Pacific-Indian Ocean Throughflow on Indian Ocean circulation and on the East Australian Current. Journal of Physical Oceanography 11 (6), 771-779.

Goodwin, N. B., Dulvy, N. K., Reynolds, J. D., 2002. Life-history correlates in the evolution of live-bearing in fishes. Philosophical Transactions of the Royal Society B: Biological Sciences 357, 259-267.

Govoni, J. J., 2005. Fisheries oceanography and the ecology of early life history of fishes: a perspective over fifty years. Scientia Marina 69 (Suppl. 1), 125-137.

Gray, C. A., 1993. Horizontal and vertical trends in the distribution of larval fishes in coastal waters off central New South Wales, Australia. Marine Biology 116, 649-666.

Gray, C. A., 1995. The influences of sewage plumes and oceanography on assemblages of larval fishes. PhD Thesis, University of Sydney, New South Wales, 439pp.

Gray, C. A., 1996. Do thermoclines explain the vertical distributions of larval fishes in the dynamic coastal waters of South-eastern Australia? Marine and Freshwater Research 47, 183-190.

Gray, C. A., Miskiewicz, A. G., 2000. Larval fish assemblages in south-east Australian coastal waters: seasonal and spatial structure. Estuarine, Coastal and Shelf Science 50, 549-570.

Gray, C. A., Kingsford, M. J., 2003. Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. Marine Ecology Progress Series 247, 211-224.

Griffin, D., Wilkin, J. L., Chubb, C. F., Pearce, A. F., Caputi, N., 2001. Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. Marine and Freshwater Research 52, 1187-1199.

Griffiths, F. B., Wadley, V. A., 1986. A synoptic comparison of fishes and crustaceans from a warm-core eddy, the East Australian Current, the Coral Sea and the Tasman Sea. Deep Sea Research Part 2 33 (11/12), 1907-1922.

Grioche, A., Koubbi, P., 1997. A preliminary study of the influence of a coastal frontal structure on ichthyoplankton assemblages in the English Channel. ICES Journal of Marine Science 54, 93-104.

Grioche, A., Koubbi, P., Harlay, X., 1999. Spatial patterns of ichthyoplankton assemblages along the Eastern English Channel French Coast during spring 1995. Estuarine, Coastal and Shelf Science 49, 141-152.

Grioche, A., Harlay, X., Koubbi, P., Fraga-Lago, L., 2000. Vertical migrations of fish larvae: Eulerian and Langrangian observations in the Eastern English Channel. Journal of Plankton Research 22, 1813-1828.

Groenkjaer, P., Wieland, K., 1997. Ontogenetic and environmental effects on vertical distribution of cod in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series 154, 91–105.

Grothues, T. M., Cowen, R., 1999. Larval fish assemblages and water mass history in a major faunal transition zone. Continental Shelf Research 19, 1171-1198.

Hanson, C. E., Pattiaratchi, C., Waite, A. M., 2005. Seasonal production regimes of south-western Australia: influence of the Capes and Leeuwin Currents on phytoplankton dynamics. Marine and Freshwater Research 56, 1011-1026.

Hare, J. A., Fahay, M. P., Cowen, R. K., 2001. Springtime ichthyoplankton of the slope region off the north-eastern United States of America: larval assemblages, relation to hydrography and implications for larval transport. Fisheries Oceanography 10(2), 164-192.

Hare, J. A., Churchill, J. H., Cowen, R. K., Berger, T. J., Cornillion, P. C., Dragos, P., Glenn, S. M., Govoni, J. J., Lee, T. N., 2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. Limnology and Oceanography 47(6), 1774-1789.

Hare, J. A., Govoni, J. J., 2005. Comparison of average larval fish vertical distributions among species exhibiting different transport pathways on the southeast United States continental shelf. Fishery Bulletin 103, 728-736

Heath, M. R., 1992. Field investigations of the early life stages of marine fish. Advances in Marine Biology. 28, 1-174.

Herzfeld, M., Tomczak, M., 1997. Numerical modelling of sea surface temperature and circulation in the Great Australian Bight. Progress in Oceanography 39(1), 29-78.

Hesp, S. A., Potter, I. C., Hall, N. G., 2002. Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. Fishery Bulletin 100, 214–227.

Hickford M. J. H., Schiel, D. R., 2003. Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Marine Ecology Progress Series 252, 255-271.

Houde, E. D., 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2, 17-29.

Hsieh, C., Chen, C., Chiu, T., 2005. Composition and abundance of copepods and ichthyoplankton in Taiwan Strait (western North Pacific) are influenced by seasonal monsoons. Marine and Freshwater Research 56, 153-161.

Huggett, J.A., Boyd, A.J., Hutchings, L., Kemp, A., 1998. Weekly variability of clupeoid eggs and larvae in the Benguela jet current: implications for recruitment. In: Pillar, S. C., Moloney, C. L., Payne, A. I. L., F.A. Shillington, F. A., (eds). 1998. Benguela Dynamics: Impacts of variability on shelf-sea environments and their living resources. South African Journal of Marine Science 7, 197-210.

Hulley, P. A., 1981. Results of the research cruise of the FRV "Walter Herwig" to South America. Family Myctophidae (Osteichthyes, Myctophiformes.) Archiv fur Fischereiwissenschaft 31(1), 1-300.

Huntsman, S. A., Brink, K. H., Barber, R. T., Blasco, D., 1981. The role of circulation and stability in controlling the relative abundance of dinoflagellates and diatoms over the Peru shelf. In Coastal Upwelling, F. A. Richards, ed., American Geophysical Union, Washington, D.C., 357-365.

Hutchings, L., Pitcher, G.C., Probyn, T.A., Bailey, G.W., 1995. The chemical and biological consequences of coastal upwelling. In: Upwelling in the Ocean. Modern Processes and Ancient Records. C.P. Summerhayes, K. Emeis,

M.V. Angel, R.L. Smith and R.L. Zeitzshel, eds. New York: John Wiley and Sons, pp. 65–82.

Hutchings, L., Barange, M., Bloomer, S. F., Boyd, A. J., Crawford, R. J. M., Huggett, J. A., Kerstan, M., Korrubel, J. L., De Oliveira, J. A. A., Painting, S. J., Richardson, S. J., Shannon, L. J., Schulein, F. H., van der Lingen, C. D., Verheye, H. M., 1998. Multiple factors affecting South African anchovy recruitment in the spawning transport and nursery areas. South African Journal of Marine Science 19, 211-225.

Hutchings, L., Beckley, L. E., Griffiths, M. H., Roberts, M. J., Sundby, S., van der Lingen, C., 2002. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Marine and Freshwater Research 53, 307-318.

Hutchins, B., Swainston, R., 1986. Sea fishes of southern Australia: complete field guide for anglers and divers. Swainston Publishing, Perth, 180pp.

Hutchins, B., 1991. Dispersal of tropical fishes to temperate seas in the southern hemisphere. Journal of the Royal Society of Western Australia 74, 79-84.

Hutchins, B., Pearce, A. F., 1994. Influence of the Leeuwin Current on recruitment of tropical reef fishes at Rottnest Island, Western Australia. Bulletin of Marine Science 54(1), 245-255.

Iles, T. D., Sinclair, M., 1982. Atlantic herring: stock discreteness and abundance. Science 215, 627-633.

Johannes, R. E., Pearce, A. F., Wiebe, W. J., Crossland, C. J., Rimmer, D. W., Smith, D. F., Manning, C., 1994. Nutrient characteristics of well-mixed coastal waters off Perth, Western Australia. Estuarine, Coastal and Shelf Science 39, 273-285.

Johannessen, A., Blom, G., Folkvord, A., Svendsen, H., 1995. The effect of local wind on the distribution of Norwegian spring spawning herring (*Clupea harengus* L.) larvae. In: Skoldal, H. R., Hopkins, C., Erikstad, K. E., Leinaas, H. P. (eds) 1995 Ecology of Fjords and Coastal Waters, pp 365-384.

Jones, C., 2006. Growth rate of sardine (*Sardinops sagax*) larvae off the oligotrophic south-western Australian coast. MSc. thesis, School of Environmental Science, Murdoch University, Western Australia, 33pp.

Jonker, L. J., 1993. Comparison of the larval fish assemblages in healthy and degraded seagrass meadows in Cockburn Sound, Western Australia. Honours thesis, School of Biological Sciences, Murdoch University, Western Australia, 47pp.

Kasai, A., Kimura, S., Nakata, H., Okazaki, Y., 2002. Entrainment of coastal water into a frontal eddy of the Kuroshio and its biological significance. Journal of Marine Systems 37, 185-198.

Kelmo, F. Attrill, M. J., Jones, M. B., 2003. Effects of the 1997–1998 El Niño on the cnidarian community of a high turbidity coral reef system (northern Bahia, Brazil). Coral Reefs, 22(4), 541-550.

Kendall, A., Naplin, N. A., 1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fishery Bulletin 79, 705-726.

Kendrick, A. J., 1993. Assemblages of larval fishes in coastal waters of south-western Australia. Honours thesis, School of Biological Sciences, Murdoch University, Western Australia, 91pp.

Kimura, S., Nakata, H. & Okazaki, Y., 2000. Biological production in mesoscale eddies caused by frontal disturbances of the Kuroshio Extension. ICES Journal of Marine Science 57, 133-142.

Kingsford, M. J., 1988. The early life history of fish in coastal waters of northern New Zealand: a review. New Zealand Journal of Marine and Freshwater Research 22, 463-479.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G., Pineda, J., 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70, 309-340.

Koné, V., Machu, E., Penven, P., Andersen, V., Garçon, V., Fréon, P., Demarcq, H., 2005. Modeling the primary and secondary productions of the southern Benguela upwelling system: A comparative study through two biogeochemical models. Global Biogeochemical Cycles 19, doi:10.1029/2004GB002427.

Koslow, J. A., Pearce, A. F., Mortimer, N., Strzelecki, J., Fearns, P., Hanson, C., Clementson, L., Kloser, R., Ryan, T., Paterson, H., Muhling, B. A., Beckley, L. E., Majewski, L., Begum, A., 2005. Biophysical oceanography off Western Australia: Dynamics across the continental shelf and slope. Chapter 5: Strategic Research Fund for the Marine Environment Interim Final Report. CSIRO, pp 143 - 213. In: Keesing, J. K., Heine, J. N. 2005. Strategic Research Fund for the Marine Environment (SRFME): Interim Final Report June 2005. CSIRO Marine and Atmospheric Research, 385pp.

Lasker, R., 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fishery Bulletin 73, 453-462.

Lasker, R., Smith, P. E., 1976. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy.

Le Clus, F., 1990. Impact and implications of large-scale environmental anomalies on the spatial distribution of spawning of the Namibian pilchard and anchovy populations. South African Journal of Marine Science 9, 141-59.

Leis, J. M., Miller, J. M., 1976. Offshore distribution patterns of Hawaiian fish larvae. Marine Biology 36, 359-367.

Leis, J. M., 1982. Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. Marine Biology 72, 89-97.

Leis, J. M., 1991. Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. Marine Biology 109, 157-166.

Leis, J. M., 1993. Larval fish assemblages near Indo-Pacific coral reefs. Bulletin of Marine Science 53(2), 362-392.

Leis, J. M., Sweatman, H. P. A., Reader, S. E., 1996. What are the pelagic stages of coral reef fishes are doing out in blue water? Daytime field observations of larval behavioural capabilities. Marine and Freshwater Research 47, 401-11.

Leis, J. M., Carson-Ewart, B. M., 1998. Complex behaviour by coral-reef fish larvae in open-water and near-reef pelagic environments. Environmental Biology of Fishes 53, 259-266.

Leis, J. M., Carson-Ewart, B. M., 2000. The larvae of Indo-Pacific coastal fishes: A guide to identification. Brill, Leiden, 850pp.

Lenanton, R. C., Joll, L., Penn, J., Jones, K., 1991. The influence of the Leeuwin Current on coastal fisheries of Western Australia. Journal of the Royal Society of Western Australia 74, 101-114.

Llanos, A., Herrera, G., Bernal, P., 1996. Prey size analysis in the diet of larvae of four clupeiform fishes in a coastal area of Central Chile. Scientia Marina 60(4), 435-442.

Lloret, J., Palomera, I., Salat, J., Sole, I., 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fisheries Oceanography 13 (2), 102-110

Lluch-Belda, D., Crawford, R. J. M., Kawasaki, T., MacCall, A. D., Parrish, R. H., Schwartzlose, R. A., and Smith, P. E., 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. South African Journal of Marine Science 8, 195-205.

Lobel, P. S., Robinson, A. R. 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. Journal of Plankton Research 10(6), 1209-1223.

Loeb, V. J., 1980. Vertical distribution and development of larval fishes in the north Pacific central gyre during summer. Fisheries Bulletin 77(4), 777-793.

Loeb, V. J., Smith, P. E., Moser, H. G. 1983. Geographical and seasonal patterns of larval fish species structure in the California Current area, 1975. CalCOFI Reports 24, 20pp.

Logerwell, E. A., Lavaniegos, B., Smith, P. E., 2001. Spatially-explicit bioenergetics of Pacific sardine in the Southern California Bight: are mesoscale eddies areas of exceptional prerecruit production? Progress in Oceanography 49, 391-406.

Logerwell, E., Smith, P. E., 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. Fisheries Oceanography 10, 13-25.

Lourey, M. J., Dunn, J. R., Waring, J., 2006. A mixed-layer climatology of Leeuwin Current and Western Australian shelf waters: Seasonal nutrient dynamics and biomass. Journal of Marine Systems 59, 25-51.

Lutjeharms, J. R., Penven, P., Roy, C., 2003. Modelling the shear edge eddies of the southern Agulhas Current, Continental Shelf Research 23, 1099-1115.

Mackas, D. L., Tsurumi, M., Galbraith, M. D., Yelland, D. R., 2005. Zooplankton distribution and dynamics in a North Pacific Eddy of coastal origin: 11. Mechanisms of eddy colonization by and retention of offshore species. Deep Sea Research Part 2 52, 1011-1035.

Mackenzie, B. R., 2000. Turbulence, larval fish ecology and fisheries recruitment: a review of field studies. Oceanologica Acta 23, 357-371.

Maillet, G. L., Checkley, D. M., 1991. Storm-related variation in the growth rate of otoliths of larval Atlantic menhaden *Brevoortia tyrannus*: a time series analysis of biological and physical variables and implications for larva growth and mortality. Marine Ecology Progress Series 79, 1-16.

Marancik, K. E., Clough, L. M., Hare, J. A., 2005. Cross-shelf and seasonal variation in larval fish assemblages on the south-east United States continental shelf off the coast of Georgia. Fishery Bulletin 103, 108-129.

Masselink, G., Pattiaratchi, C.B., 1998. The effect of sea breeze on beach morphology, surf zone hydrodynamics and sediment resuspension. Marine Geology 146, 115-135.

Masselink, G., Pattiaratchi, C.B., 2001. Characteristics of the sea breeze system in Perth, Western Australia, and its effect on the nearshore wave climate. Journal of Coastal Research 17(1), 173-187.

Matsuura, Y., De Silva Garcia, A. C., Katsuragawa, M., Suzuki, K., 1993. Distribution and abundance of two species of codlet (Teleostei, Bregmacerotidae) larvae from the south-eastern Brazilian Bight. Fisheries Oceanography 2(2), 82-90.

McClatchie, S., Middleton, J. F., Ward, T. M., 2005. Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight. Journal of Geophysical Research 31, 1-9.

McGillicuddy, D. J. Jr, Robinson, A. R., 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. Deep Sea Research Part 2 44,1427-1450.

McKinnon, A. D., Meekan, M. G., Carleton, J. H., Furnas, M. J., Duggan, S., Skirving, W., 2003. Rapid changes in shelf waters and pelagic communities on the southern Northwest Shelf Australia, following a tropical cyclone. Continental Shelf Research 23, 93-111.

Miller, L. A., Robert, M., Crawford, W. R., 2005. The large, westward-propagating Haida Eddies of the Pacific eastern boundary. Deep Sea Research Part 2 52, 845-851.

Mizobata, K., Saitoh, S. I., Shiomoto, A., Miyamura, T., Shiga, N., Imai, K., Toratani, M., Kajiwara, Y., Sasaoka, K., 2002. Bering Sea cyclonic and anti-cyclonic eddies observed during summer 2000 and 2001. Progress in Oceanography 55, 65-75.

Moku, M., Tsuda, A., Kawaguchi, K., 2003. Spawning season and migration if the Myctophid fish *Diaphus theta* in the western north Pacific. Ichthyological Research 50(1), 52-58.

Moran, M., Burton, C., Jenke, J., 2003. Long-term movement patterns of continental shelf and inner gulf snapper (*Pagrus auratus*, Sparidae) from tagging in the Shark Bay region of Western Australia. Marine and Freshwater Research 54, 913-922.

Morgan, G. J., Wells, F. E., 1991. Zoogeographic provinces of the Humboldt, Benguela and Leeuwin Current systems. Journal of the Royal Society of Western Australia 74, 59-69.

Morrow, R., Fang, F., Fieux, M., Molcard, R., 2003. Anatomy of three warm-core Leeuwin Current eddies. Deep Sea Research Part 2, 50 (12-13), 2229-2243.

Moser, H. G., Ahlstrom, E. H., 1974. Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, a case study. Fishery Bulletin 72(2), 391-413.

Moser, H. G., Ahlstrom, E. H., Paxton, J. R., 1984. Myctophidae: Development. In Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Jendall Jr. A. W., Richardson, S. L. (eds), 1984. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists, Special Publication 1, 760 pp.

Moser, H. G., Boehlert, G. W., 1991. Ecology of pelagic larvae of juveniles of the genus *Sebastes*. Environmental Biology of Fishes 30,203-224.

Moser, H. G., Smith, P. E., 1993. Larval fish assemblages and oceanic boundaries. Bulletin of Marine Science 53, 283-289.

Moser, H. G., Watson, W., 2005. Myctophidae: Lanternfishes. In Richards, W. J., (ed). 2006. Early stages of Atlantic fishes: An identification guide for the Western Central North Atlantic, Volume 1, Taylor and Francis Group, USA, 2 640 pp.

Mullin, M. M., Brook, E. R., Reid, F. M. H., Napp, J., Stewart, E. F., 1985. Vertical structure of nearshore plankton off Southern California: a storm and a larval fish food web. Fishery Bulletin 83, 151-170.

Munk, P., Bjornsen, P. K., Boonruang, P., Fryd, M., Hansen, P. J., Janekarn, V., Limtrakulvong, V., Nielsen, T. G., Hansen, O. S., Satapoomin, S., Sawangarreruks, S., Thomsen, H. A., Ostergaard, J. B., 2004. Assemblages of fish larvae and mesozooplankton across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). Marine Ecology Progress Series 274, 87-97.

Nafpaktitus, B. G., 1978. Systematics and distribution of lanternfishes of the genera *Lobianchia* and *Diaphus* (Family Myctophidae) in the Indian Ocean. Natural History Museum of Los Angeles County Science Bulletin 30, 1-99.

Nakata, H., Kimura, S., Okazaki, Y., Kasai, A., 2000. Implications of mesoscale eddies caused by frontal disturbances of the Kuroshio Current for anchovy recruitment. ICES Journal of Marine Science 57, 143-152.

Neira, F. J., Potter, I. C., 1992. The ichthyoplankton of a seasonally closed estuary in temperate Australia. Does an extended period of opening influence species composition? Journal of Fish Biology 41, 935-953.

Neira, F. J., Potter, I. C., Bradley, J. S., 1992. Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. Marine Biology 112, 1-16.

Neira, F. J., Miskiewicz, A. G., Trnski, T., 1998. Larvae of temperate Australian fishes: Laboratory guide for larval fish identification. University of Western Australia Press, 474pp.

Nilsson, C. S., Cresswell, G. R., 1981. The formation and evolution of East Australian Current warm-core eddies. Progress in Oceanography 9, 133-183.

Nishimoto, M. M., Washburn, L., 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Marine Ecology Progress Series 241, 183-199.

Okazaki, Y., Nakata, H., Kimura, S., 2002. Effects of frontal eddies on the distribution and food availability of anchovy larvae in the Kuroshio Extension. Marine and Freshwater Research 53, 403-410.

Olivar, M. P., 1987. Larval development and spawning of *Diaphus hudsoni* in the Benguela Current region, Marine Biology 94(4), 605-611.

Olivar M. P., Shelton, P. A., 1993. Larval fish assemblages of the Benguela Current. Bulletin of Marine Science 53(2), 450-474.

Olivar, M. P., Beckley, L. E., 1994. Influence of the Agulhas Current on the distribution of lanternfish larvae off the south-east coast of Africa. Journal of Plankton Research 16, 1759-1780.

Olivar, M. P., Sabates, A., 1997. Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. Marine Biology 129, 289-300.

Olivar, M. P., Moser, H. G., Beckley, L. E., 1999. Lanternfish larvae from the Agulhas Current (SW Indian Ocean). Scientia Marina 63(2), 101-120.

Olivar, M. P., Salat, J., Palomera, I., 2001. Comparative study of spatial distribution patterns of early stages of anchovy and pilchard in the NW Mediterranean Sea. Marine Ecology Progress Series 217, 111-120.

Olivar, M. P., Catalana, I. A., Emelianova, M., Fernandez de Puellesba, M. L., 2003. Early stages of *Sardina pilchardus* and environmental anomalies in the Northwestern Mediterranean. Estuarine, Coastal and Shelf Science 56, 609-619.

Painting, S. J., Hutchings, L., Huggett, J. A., Korrubel, J. L., Richardson, A. J., Verheye, H. M., 1998. Environmental and biological monitoring for forecasting anchovy recruitment in the southern Benguela upwelling region. Fisheries Oceanography 7, 364-374.

Palomera, I., Olivar, M. P., 1996. Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). Publicaciones Especiales, Instituto Espanol de Oceanografia 22, 71-75.

Parrish, H. R. H., Nelson, C. S., Bakun, A., 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biological Oceanography 1, 175–203.

Parrish, R. H., Serra, R., Grant, W. S., 1989. The monotypic sardines, *Sardina* and *Sardinops*: Their taxonomy, distribution, stock structure, and zoogeography. Canadian Journal of Fisheries and Aquatic Sciences 46(11), 2019-2036.

Paterson, H., 2006. Microzooplankton from the Two Rocks transect of south west, Western Australia: Biomass, diversity and impact on phytoplankton. PhD thesis, School of Animal Biology, University of Western Australia.

Paxton, J. R., Hoese, D. F., Allen, G. R., Hanley, J. E., 1989. Zoological catalogue of Australia: Pisces Petromyzontidae to Carangidae. Canberra: Australian Government Publishing Service 7, 665pp.

Pearce, A.F., Phillips, B.F., 1988. ENSO events, the Leeuwin Current and larval recruitment of the Western Rock Lobster. Journal du Conseil 45, 13-21

Pearce, A. F., 1991. Eastern boundary currents of the southern hemisphere. Journal of the royal society of Western Australia 74, 1-14.

Pearce, A. F., Griffiths, R. W., 1991. The mesoscale structure of the Leeuwin Current: A comparison of laboratory models and satellite images. Journal of Geophysical Research 96, 16739-16757.

Pearce, A. F., Pattiaratchi, C., 1999. The Capes Current: a summer countercurrent flowing past Cape Leeuwin and Cape Naturaliste, Western Australia. Continental Shelf Research 19, 401-420.

Pearce, A., Helleren, S., Marinelli, M., 2000. Review of productivity levels of Western Australian coastal and estuarine waters for mariculture planning purposes. Fisheries Western Australia Research Report No. 123. Fisheries Western Australia, Perth, 71pp.

Pearce, A. F. Feng, M., Fandry, C., Koslow, J. A., Mortimer, N., Fearns, P., in press. Structure and dynamics of the pelagic ecosystem off south-western Australia. Continental Shelf Research.

Porter, S. M., Ciannelli, L., Hillgruber, N., Bailey, K. M., Chan, K. S., Canino, M. F., Haldorson, L. J., 2005. Environmental factors influencing larval walleye Pollock *Theragra chalcogramma* feeding in Alaskan waters. Marine Ecology Progress Series 302, 207-217.

Quartly, G. D., Srokosz, M. A., 2004. Eddies in the Southern Mozambique Channel. Deep Sea Research Part 2 51, 69-83.

Richards, W. J. (ed). 2006a. Early stages of Atlantic fishes: An identification guide for the Western Central North Atlantic. Taylor and Francis, 2 640pp.

Richards, W. J., 2006b. Phosichithydae: Lighfishes. In Richards, W. J. (ed). 2006. Early stages of Atlantic fishes: An identification guide for the Western Central North Atlantic, Chapter 18, Taylor and Francis, 2 640pp.

Richardson, K., Gissel Nielsen, T., Bo Pedersen, F., Heilmann, J.P., Løkkegård, B., Kaas, H., 1998. Spatial heterogeneity in the structure of the planktonic food web in the North Sea. Marine Ecology Progress Series 168, 197–211.

Ridgway, K. R., Condie, S. A., 2004. The 5500km-long boundary flow off western and southern Australia. Journal of Geophysical Research 109, C04017 doi: 10.1029/2003JC001921.

Rodriguez, J. M., Hernandez-Leon, S., Barton, E. D., 1999. Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. Deep Sea Research Part 1 46, 1969-1984.

Rodriguez, J. M., Barton, E. D., Hernandez-Leon, S., Aristegui, J. 2004. The influence of mesoscale physical processes on the larval fish community in the Canaries CTZ, in summer. Progress in Oceanography 62, 171-188.

Rogers, P. J., Geddes, M., Ward, T. M., 2003. Blue sprat *Spratelloides robustus* (Clupeidae: Dussumieriinae): a temperate clupeoid with a tropical life history strategy? Marine Biology 142: 809-824.

Röpke, A., 1993. Do larvae of mesopelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients? Marine Ecology Progress Series 101, 223-235.

Sabates, A., 2004 Diel vertical distribution of fish larvae during the winter-mixing period in the Northwestern Mediterranean, ICES Journal of Marine Science 61, 1243-1252.

Sabates, A., Salat, J., Maso, M., 2004. Spatial heterogeneity of fish larvae across a meandering current in the northwestern Mediterranean. Deep Sea Research Part 1 51, 545-557.

Sampey, A., Meekan, M. G., Carleton, J. H., McKinnon, A. D., McCormick, M. I., 2004. Temporal patterns in distributions of tropical fish larvae on the North-west Shelf of Australia. Marine and Freshwater Research 55, 473-487.

Sanchez-Velaso, L., Shirasago, B., Cisneros-Mata, M. A., Avalos-Garcia, C., 2000. Spatial distribution of small pelagic fish larvae in the Gulf of California and its relation to the El Niño 1997-1998. Journal of Plankton Research 22, 1611-1618.

Sanchez-Velaso, L., Valdez-Holguin, J. E., Shirasago, B., Cisneros-Mata, M. A., Zarate, A., 2002. Changes in the spawning environment of *Sardinops caeruleus* in the Gulf of California during El Niño 1997-1998. Estuarine, Coastal and Shelf Science 54, 207-217.

Sanchez-Velaso, L., Avalos-Garcia, C., Renteria-Cano, M., Shirasago, B., 2004a. Fish larvae abundance and distribution in the central Gulf of California during strong environmental changes (1997-1998 El Niño and 1998-1999 La Niña). Deep Sea Research Part 2 51, 711-722.

Sanchez-Velaso, L., Jiminez-Rosenberg, S. P. A., Shirasago, B., Obeso-Nieblas, M., 2004b. Distribution and abundance of fish larvae in Bahia de la Paz (Gulf

of California) and their relation to hydrographic variability during summer (1997-1998). Deep Sea Research Part 2 51, 723-737.

Santos, A. M. P., Peliz, A., Dubert, J., Oliveira, P. B., Angelico, M. M., Re, P., 2004. Impact of a winter upwelling event on the distribution and transport of sardine (*Sardina pilchardus*) eggs and larvae off western Iberia: a retention mechanism. Continental Shelf Research 24, 149-165.

Sanvicente-Anorve, L., Flores-Coto, C., Chiappa-Carrara, X., 2000. Temporal and spatial scales of ichthyoplankton distribution in the southern Gulf of Mexico. Estuarine, Coastal and Shelf Science 51, 463-475.

Sassa, C., Kawaguchi, K., 2004. Larval feeding habits of *Diaphus garmani* and *Myctophum asperum* (Pisces: Myctophidae) in the transition region of the western North Pacific. Marine Ecology Progress Series 278, 279-290.

Sassa, C., Kawaguchi, K., Hirota, Y., Ishida, M., 2004a. Distribution patterns of larval myctophid fish assemblages in the sub-tropical-tropical waters of the western North Pacific, Fisheries Oceanography 13(4), 267-282.

Sassa, C., Kawaguchi, K., Mori, K., 2004b. Late winter larval mesopelagic fish assemblage in the Kuroshio waters of the western North Pacific. Fisheries Oceanography 13, 121-133.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S. E., MacCall, A. D., Matsuura, Y., Nevarez-Martinez, M. O., Parrish, R. H., Roy, C., Serra, R., Shust, K. V., Ward, M. N., Zuzunaga, J. Z., 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21, 289-348.

Simpson, J. J., 1987. Transport processes affecting the survival of pelagic fish stocks in the California Current. In: 10th Annual Larval Fish Conference: American Fisheries Society Symposium 2. American Fisheries Society, 39-59.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Program, University of Washington Press, 259pp.

Smith, K. A., 2000. Active and passive dispersal of *Centroberyx affinis* (Berycidae) and *Gonorynchus greyii* (Gonorynchidae) larvae on the Sydney shelf. Marine and Freshwater Research 51, 229-234.

Smith, K. A., Gibbs, M. T., Middleton, J. H., Suthers, I. M., 1999. Short-term variability in larval fish assemblages of the Sydney shelf: tracers of hydrographic variability. Marine Ecology Progress Series 178, 1-15.

Smith, K. A., Suthers, I. M., 1999. Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. Marine Ecology Progress Series 176, 49-62.

Smith, P. E., Horne, J. K., Schneider, D. C., 2001. Spatial dynamics of anchovy, sardine and hake pre-recuit stages in the California Current. ICES Journal of Marine Science 58, 1063-1071.

Smith, P. E., Moser, H. G., 2003. Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current Region. Deep Sea Research Part 2 50, 2519-2536.

Somarakis, S., Ganias, K., Siapatis, A., Koutsikopoulos, C., Machias, A., Papaconstantinou, C., 2006. Spawning habitat and daily egg production of

sardine (*Sardina pilchardus*) in the eastern Mediterranean. Fisheries Oceanography doi: 10.1111/j.1365-2419.2005.00387.x

Somarakis, S., Ganias, K., Tserpes, G., Koutsikopoulos, C., 2004. Ovarian allometry and the use of the gonadosomatic index: a case study in the Mediterranean sardine, *Sardina pilchardus*. Marine Biology 146, 181-189.

Stevenik, E. K., Sundby, S., Cloete, R., 2001. Influence of buoyancy and vertical distribution of sardine *Sardinops sagax* eggs and larvae on their transport in the northern Benguela ecosystem. South African Journal of Marine Science 23, 85-98.

Suthers, I. M., Frank, K. T., 1991. Comparative persistence of marine fish larvae from pelagic versus demersal eggs off south-western Nova Scotia, Canada, Marine Biology 108(2), 175-184.

Tranter, D. J., Parker, R. R., Cresswell, G. R., 1980. Are warm-core eddies unproductive? Nature 284, 540-542.

Tsai, C., Chen, P., Chen, C., Lee, M., Shiah, G., Lee, K., 1997. Fluctuations in abundance of larval anchovy and environmental conditions in coastal waters off south-western Taiwan as associated with the El Niño-Southern Oscillation. Fisheries Oceanography 6, 238-249.

Uehara, S., Syahailatua, A., Suthers, I. M., 2005. Recent growth rate of larval pilchards *Sardinops sagax* in relation to their stable isotope composition, in an upwelling zone of the East Australian Current. Marine and Freshwater Research 56, 549-560.

Urho, L., 1999. Relationship between dispersal of larvae and nursery areas in the Baltic Sea. ICES Journal of Marine Science 56, 114-121.

van der Lingen, C. D., Checkley, D. Jr, Barange, M., Hutchings, L., Osgood, K., 1998. Assessing the abundance and distribution of eggs of sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, on the western Agulhas Bank, South Africa, using a continuous, underway fish egg sampler. Fisheries Oceanography 7(1), 35-47.

Vélez, J. A., Watson, W., Arntz, W., Wolf, M., Schnack-Schiell, S. B., 2005. Larval fish assemblages in Independencia Bay, Pisco, Peru: temporal and spatial relationships. Marine Biology 147(1), 77-91

Waite, A. M., Muhling, B. A., Holl, C., Thompson, P., Beckley, L. E., Montoya, J., Pesant, S., Strzelecki, J., submitted a. Food web structure in two counter-rotating eddies based on δN^{15} and δC^{13} isotopic analyses. Deep Sea Research Part 2.

Waite, A. M., Griffin, D. A., Pesant, S., Feng, M., Thompson, P. A., Beckley, L. E., Domingues, C., Gaughan, D., Hanson, C., Holl, C., Koslow, J. A., Meuleners, M., Montoya, J., Moore, T., Muhling, B. A., Paterson, H., Rennie, S., Srzelecki, J., Twomey, L., submitted b. The Leeuwin Current and its eddies: an overview. Deep Sea Research Part 2.

Ward, T. M., Staunton-Smith, J., 2002. Comparison of the spawning patterns and fisheries biology of the sardine, *Sardinops sagax* in temperate South Australia and sub-tropical southern Queensland. Fisheries Research 56, 37-49.

Ward, T. M., Staunton-Smith, J., Hoyle, S., Halliday, I. A., 2003. Spawning patterns of four species of predominantly temperate pelagic fishes in the sub-tropical waters of southern Queensland. Estuarine, Coastal and Shelf Science 56, 1125-1140.

Ward, T. M., McLeay, L. J., Dimmlich, W. F., Rogers, P. J., McClatchie, S., Matthews, R., Kampf, J., van Ruth, P. D. 2006. Pelagic ecology of a northern boundary current system: effects of upwelling on the production and distribution of sardine (*Sardinops sagax*), anchovy (*Engraulis australis*) and southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. Fisheries Oceanography 15 (3), 191-207.

Woo, M., Pattiaratchi, C., Schroder, W. submitted. Hydrography and water masses off the Western Australian coast. Ocean Dynamics.

Woo, M., Pattiaratchi, C., Schroeder, W. 2006. Summer surface circulation along the Gascoyne continental shelf, Western Australia. Continental Shelf Research 26, 132-152.

Yimin, M., Lyons, T. J., Blockley, J. A., 2001. Surface influences on the Australian West Coast Trough. Theoretical and Applied Climatology, 68, 207-217.